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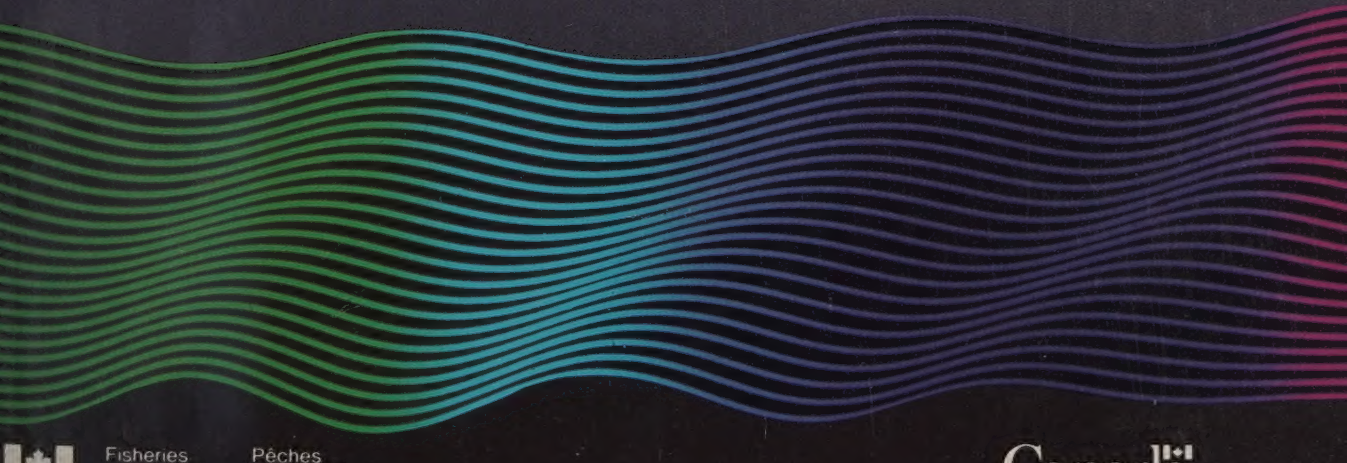

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Estimating Coho Salmon (*Oncorhynchus kisutch*) Spawning Escapements by Conducting Visual Surveys in Areas Selected Using Stratified Random and Stratified Index Sampling Designs

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Irvine, J. R., R. C. Bocking, K. K. English, and M. Labelle. 1992. Estimating coho salmon (*Oncorhynchus kisutch*) spawning escapements by conducting visual surveys in areas selected using stratified random and stratified index sampling designs. Can. J. Fish. Aquat. Sci. 49: 1972–1981.

Spawning escapement estimates were obtained for adult and jack (precocious male) coho salmon (*Oncorhynchus kisutch*) by conducting visual surveys on foot in stream reaches selected by stratified random and stratified index sampling designs. The approach was evaluated for three years in two streams with widely varying escapements; estimates of adult escapements using the stratified index design were always similar to estimates obtained through an independent mark–recapture program. The stratified random design underestimated escapement in every case but one. Because the distribution of fish was aggregated, with random sampling there was a higher probability of sampling low fish abundance areas than high-abundance areas. Numbers of jack coho were underestimated with each sampling design, probably because we overestimated our efficiency of seeing these fish. When using this approach, the efficiency of observing fish during surveys and the length of time salmon are alive in the survey area should be estimated; the latter for our survey areas ranged between 13 and 17 d with one exception (8 d). Labour costs associated with estimating escapements to our streams by visual survey indexing techniques were less than by mark–recapture or by operating fish counting fences.

On a obtenu des estimations de l'échappée d'adultes et de jeunes mâles précoces de saumon coho (*Oncorhynchus kisutch*) lors de relevés visuels à pied menés dans des tronçons de cours d'eau choisis selon des plans d'échantillonnage aléatoire stratifié et d'échantillonnage de classification stratifié. Cette approche a été évaluée pendant trois ans dans deux cours d'eau à échappée nettement différente. On a découvert que les estimations de l'échappée d'adultes basées sur un plan d'échantillonnage de classification stratifié étaient toujours semblables aux estimations obtenues par l'entremise d'un programme indépendant de marquage et de recapture. Par contre, le plan d'échantillonnage aléatoire stratifié a sous-estimé l'échappée dans tous les cas sauf un. Étant donné que les poissons étaient groupés en bancs, la probabilité d'échantillonner des zones de faible abondance du saumon était plus élevée dans le cas de l'échantillonnage aléatoire. Le nombre de jeunes mâles précoces a été sous-estimé dans les deux cas, probablement parce que l'efficacité d'identifier ces poissons a été surestimée. Si l'on utilise l'approche décrite, on devrait estimer l'efficacité de l'observation des poissons au cours des relevés et la durée de vie des saumons dans la zone expérimentale. Au cours de la présente étude, la durée de vie a varié de 13 à 17 d, sauf dans un cas (8 d). Les coûts de la main-d'oeuvre liés à l'estimation de l'échappée dans ces cours d'eau lors de relevés visuels à pied étaient moins élevés que des programmes de marquage et recapture ou l'exploitation de barrages de dénombrement des poissons.

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Numbers of coho salmon (*Oncorhynchus kisutch*) returning to spawn in British Columbian streams are generally estimated by fishery officers employed by the Department of Fisheries and Oceans who conduct visual surveys (Waldichuk 1984). Because of time and budget limitations, it is rarely possible for these officers to survey an entire stream. Typically, fishery officers walk some portion(s) of a stream, count or estimate numbers of live and/or dead fish, and expand these numbers using often unspecified techniques to obtain an estimate of spawning escapement. The accuracy of spawning escapement estimates obtained using this approach varies considerably. As a result, caution must be exercised when comparing escapement estimates among streams, or among years for particular streams (Serbic 1991). Escapement estimates for coho salmon are especially prone to error because adult coho in streams tend not to occur in high densities, and their cryptic colouration makes them difficult to see.

The need for more accurate and precise salmon escapement estimates, and the standardization of estimation procedures, has been well documented (Walters and Ludwig 1981; Pearse 1982; Symons and Waldichuk 1984). Accurate estimates of spawning stocks are required to assess whether stock sizes and harvest rates are optimal. Precision or consistency of escapement estimates is required if fishery managers are to have confidence in the data and may be more important than accuracy for defining long-term stock–recruitment relationships (Symons and Waldichuk 1984).

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To improve the accuracy and precision of escapement estimates obtained using visual surveys, a variety of sampling approaches can be used to identify portions of a stream to survey for fish. The simplest approach may be to use a simple random sampling design. With this design, each section of a stream has an equal probability of being selected. However, if sampling units can be divided into homogeneous groups, then stratified random sampling (SRS) is generally preferable to simple random sampling, since stratification usually results in a smaller variance than that given by comparable simple random sampling (Cochran 1977). A SRS design to estimate escapement is achieved by stratifying the watershed and then randomly selecting sample sites within each stratum. Alternatively, sample units within each stratum can be selected on the basis of easy access by surveyors and/or on the basis of expected or actual locations of fish. This latter type of sampling has been termed stratified index sampling (SIS) (Johnston et al. 1987; Bocking et al. 1988).

In this study we evaluated SRS and SIS for estimating numbers of coho salmon returning to two streams on Vancouver Island. Visual surveys in both streams were conducted in areas determined using each sampling design during 1987, 1988, and 1989. We determined escapements using the area-under-the-curve method (Beidler and Nickelson 1980; Ames 1984; Tschaplinski and Hyatt 1990; English et al. 1992). With this method, fish numbers in a watershed are estimated at intervals during the spawning season. The area-under-the-curve of fish numbers versus time is divided by an estimate of the mean time fish spend alive in the study area to yield an estimate of escapement.

There were numerous factors considered in selecting streams in which to carry out the study. We wanted to ensure that our results and any approaches that we developed would have practical value. We therefore wanted to encounter situations similar to those faced by other enumerators of coho salmon, namely fish should be dispersed throughout the watersheds, access along the streams should be limited, rapid changes in water levels with concomitant changes in water clarity should occur during the spawning season, and habitat attributes within the streams should be variable and difficult to survey. An additional consideration was that the streams should have an independent escapement estimation program in place.

Study Areas

Two streams were chosen along the east coast of Vancouver Island for the study, Black Creek and French Creek. Each stream was known to have significant numbers of coho that returned to spawn in widely dispersed locations throughout each watershed. As well, a separate project (Labelle 1990a, 1990b) was underway which would produce independent mark–recapture escapement estimates.

Black Creek (Fig. 1) is a low-gradient stream approximately 26 km long and 5–6 m wide in its middle reaches. For most of its length, it meanders through agricultural land, small lakes, swampy areas, and beaver ponds. In the lower watershed, there are several tributaries including Millar Creek. A maximum discharge of 60 $\mathrm{m^3{\cdot}s^{-1}}$ has been recorded during floods. Black Creek supports populations of coho salmon, cutthroat trout (*Oncorhynchus clarki*), and steelhead trout (*Oncorhynchus mykiss*). Annual escapement estimates for coho are highly variable, ranging from as low as 750 spawners in recent years to more than 15 000 prior to 1975 (Hancock and Marshall 1985; Clark and Irvine 1989; Labelle 1990a). Coho spawn throughout the watershed, but the best spawning grounds are in Millar Creek, near the middle of Stratum C, and in the lower portion of Stratum F (Fig. 1).

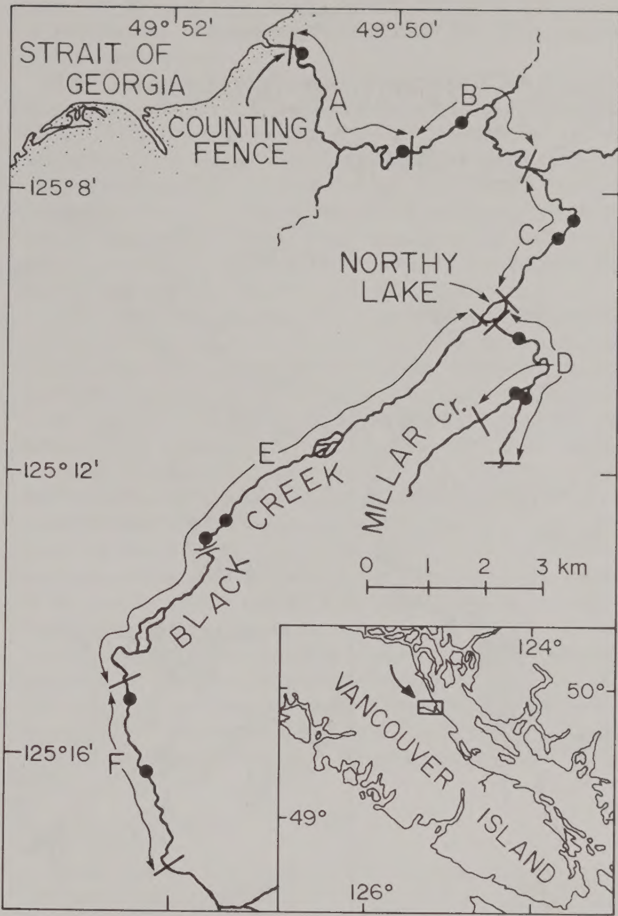

FIG. 1. Map of Black Creek drainage showing location of strata (A–F), index sites (●), and the fish counting fence. Inset shows the location of the study site on Vancouver Island, British Columbia.

French Creek is also a small stream draining the southeast side of Vancouver Island (Fig. 2). This stream is approximately 20 km long and averages 12 m in width in its middle sections. The creek bifurcates approximately 12.5 km upstream from the estuary, with only the lower part of the western fork being accessible to anadromous fish because of a 15-m waterfall about 400 m above the bifurcation. Anadromous fish have access to most of the eastern fork. French Creek has many pools and large seasonal fluctuations in water levels. Stream discharge can exceed 100 $\mathrm{m^3{\cdot}s^{-1}}$ during winter and usually decreases to negligible amounts during summer. French Creek also supports populations of coho salmon and cutthroat and steelhead trout. In addition, a small number of chum salmon (*Oncorhynchus*

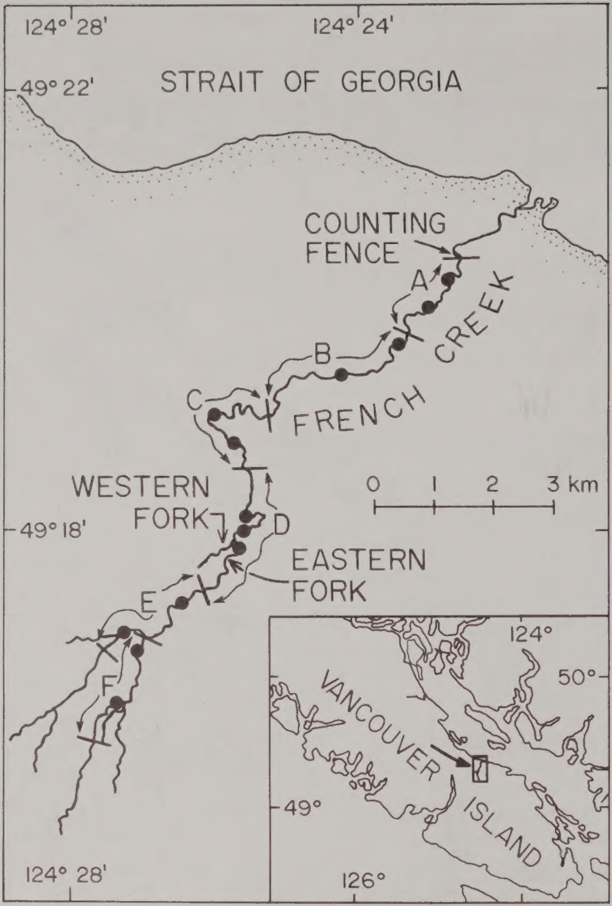

FIG. 2. Map of French Creek showing location of strata (A–F), index sites (●), and the fish counting fence. Inset shows the location of the study site on Vancouver Island, British Columbia.

keta) spawn during most years in the lower creek. Annual escapement estimates for coho have ranged from 107 adults in 1987 to over 3500 fish in 1977 (Hancock and Marshall 1985; Labelle 1990a). The best spawning areas for coho are near the confluence of the two main forks and at scattered locations within Strata E and F (Fig. 2).

Methods

Fish Enumeration Fences and Mark–Recapture Escapement Estimates

Collapsible fish counting fences near the stream mouths of both systems provided us with the means of estimating escapements independently from our indexing study (Labelle 1990a). The fences and associated fish traps were always installed and operating well before any fish had moved upstream and they were manned 7 d a week. Fish captured were dip-netted out of the traps, examined, marked, and released upstream from the fence. In 1987 and 1988, the operculum of each coho captured was marked using a hole punch, and in 1989, the operculum of each coho was marked with individually numbered chick wing tags (Ketchum Manufacturing Sales Ltd.). We also determined the sex of the fish and identified and recorded each fish as a jack (precocious male having spent less than 1 yr in the ocean) or an adult.

Complete counts of all upstream-migrating coho at the fences were never achieved because small coho could pass through the fence panels undetected and because the fences occasionally had to be collapsed during periods of high water and fish could pass by undetected at these times. The number of fish processed at each fence, plus the number of unmarked fish recovered during all surveys conducted upstream of the fences, provided a minimum estimate of the number of fish escaping to each stream. To estimate the total escapement, a mark–recapture program was conducted.

Recoveries of marked and unmarked fish upstream of the fences were made throughout each season by an experienced field crew using an electrofisher. Although the voltage and frequency settings on the electrofishers varied, to minimize deleterious effects on fish, settings were as low as possible (usually 200–300 V and 15–60 cycles) so that fish were only temporarily stunned. A second person operated a dip net behind the person with the electrofisher, and in some instances two other people operated a seine net downstream of this crew. In each system, several sampling sites were selected based on site accessibility and the availability of fish. Fish were never sampled on or near redds. Each fish caught was examined for opercular marks, given a secondary mark, and released. In 1987, 1988, and 1989 respectively, recoveries were made on 3, 9, and 5 occasions in Black Creek and 4, 13, and 8 occasions in French Creek.

To estimate total escapement, three mark–recapture models were used. The first method was an open model which was developed specifically to estimate escapement to these streams and which has been described in detail by Labelle (1990a, 1990b). This escapement simulation model uses daily fish counts at the fences, stream census data, and information on the timing of floods to numerically reconstruct the buildup and decline of the coho population in each stream. The model predicts the numbers of marked and unmarked fish in the stream based on a hypothesized period of stream residency. The discrepancy between expected marked ratios and the actual ratios obtained during the stream surveys is quantified. The combination of population size and stream residence time which best fits the time series of marked proportions identifies the maximum likelihood estimate of escapement. The likelihood ratio method is used to generate upper and lower bounds around each estimate (Labelle 1990a).

Two closed models were also used to generate escapement estimates. Stream census data were combined and pooled Petersen estimates (Seber 1982) were generated for each system annually. As well, escapements were estimated using a sequential Bayesian algorithm described by Gazey and Staley (1986).

Stratified Sampling Designs for Visual Survey Escapement Estimates

To define the sampling universe for SRS, and to select the sites for SIS, each stream was surveyed during early autumn. All of French Creek was accessible to us, but access was poor to some portions of the Black Creek watershed (Northy Lake and swamp areas immediately upstream). Six strata were selected for each system (Fig. 1 and 2). The locations of stratum boundaries were determined by tributary confluences and/or major transitions in stream gradient or some other habitat characteristic. Numerical simulations based on fish density and distribution pattern data defined an optimum survey unit length of

250 m (Bocking et al. 1988). The sampling universe for random sampling in French Creek consisted of all 250-m units in each stratum. The sampling universe for Black Creek was restricted to those 250-m units in each stratum that were accessible to us.

We restricted the total number of sites to what we considered would be realistic in operational rather than research assessments. Two sites were randomly chosen from each stratum for each survey. Random sites selected for one survey were available for selection in subsequent surveys.

In selecting index sites, consideration was given to site accessibility, as well as how representative of the stratum the site was in terms of substrate particle size, gradient, cover, and the anticipated use by mature coho (Bocking et al. 1988). Usually, two index sites were selected per stratum, but Stratum D in each creek had three index sites, and Stratum B in Black Creek, where fish were rarely seen and access was extremely poor, contained only one index site. An attempt was made to select index sites within each stratum that included both good and marginal habitat for fish spawning and holding.

The number of surveys conducted each year was influenced by hydrological conditions and the numbers of fish seen. Surveys were usually conducted at 5- to 7-d intervals until the total number of coho observed during the last survey was negligible (<2). Surveys commenced as soon as possible following the first significant passage of coho through the counting fences. In 1987, all index and random survey units were sampled five times in Black Creek and three times in French Creek. In 1988, seven surveys were made at Black Creek and six at French Creek, and in 1989, eight surveys were made at Black Creek and seven at French Creek.

Visual Surveys

Fish were counted by two observers walking upstream through each survey area. The observers carried 2-m-long poles to displace coho salmon hiding under cutbanks, rocks, and debris. In narrow sections, one observer walked behind the other; in wider sections, they walked one on each side of the stream. When coho were disturbed, their densities were usually low enough that the movements of individual fish could be followed, and therefore, double counting was unlikely. Surveys were only conducted when flow conditions permitted good visibility and safe wading. It generally took 3–4 d to conduct a complete survey (SIS and SRS sites) of each stream. We usually surveyed three random and three index sites on each day. In the few instances when weather conditions prevented us from conducting surveys in each strata, fish numbers in unsampled strata were derived from a linear interpolation between the abundances observed on the previous and following surveys when these strata were sampled.

Observer Efficiency

The efficiency of observing coho during visual surveys was estimated by comparing counts with electrofisher catches. We attempted to obtain observer efficiency estimates over a wide range of habitat conditions in each stream. To measure observer efficiency, within 1 h of a regular visual survey in a 250-m section of stream, a separate crew estimated the number of coho using an electrofisher. The same approach in the field was used as described earlier for the mark–recapture surveys, except that in some cases where portions of a stream were too deep to sample efficiently with an electrofisher, a snorkeller with a dive light also estimated coho numbers. Where practical, survey sections were blocked with nets to prevent fish movement out of or into the area. Separate counts were made for adult and jack coho in each section.

In evaluating observer efficiency, the number of fish observed (dependent variable) was assumed to be a function of the number of fish present as estimated by the electrofisher counts (independent variable). We only used data from survey sections where at least one fish was observed by either method. In some instances the number of fish observed was greater than the number of fish caught. In these cases, because it was known that the number of fish caught underestimated the fish present, the number caught was replaced by the number observed.

Although the experimental design called for age- and system-specific observer efficiency relationships to be determined each year, we were often unable to conduct sufficient tests to accomplish this. Physical conditions in the two streams were different, so we analyzed observer efficiency data for Black Creek and French Creek separately. Adult coho were much more readily observed than jack coho, so it appeared that data for the two age classes should be analyzed separately. To statistically determine whether separate regression equations should be computed for the different age classes and years, we carried out analyses of covariance. In the analyses of covariance, the greater of the number of fish electrofished and the number observed during visual surveys was the covariate and the year or age class was the treatment. The significance of the interaction between the covariate and the treatment was used to determine whether the slopes of the various regression lines were different (Wilkinson 1988). To determine the desirability of transforming the data, we examined distributions of the residuals ($Y - \hat{Y}$) (Zar 1984).

Residence Time

The estimation of escapement using the area-under-the-curve method requires an estimate of the average time coho spend in the survey area (survey life or residence time) (Perrin and Irvine 1990; English et al. 1992). At French Creek, the survey area was the entire stream area upstream of the counting fence, but at Black Creek, the survey area excluded those sections inaccessible to us.

Residence time was determined in Black Creek (1987, 1988, and 1989) and French Creek (1988 and 1989) by tagging groups of adult coho with dull-coloured Petersen disks (1987 and 1989) or spaghetti tags (1988) as the fish passed the counting fences. Counts of tagged fish were recorded during subsequent visual surveys. For each survey, numbers of tagged fish observed at each site were corrected for observer efficiency and, when necessary, tag retention. Because an operculum of each fish tagged with a Petersen or spaghetti tag was marked, we were able to estimate tag retention by calculating, from carcass recoveries and fish examined during electrofishing surveys, the frequency with which opercular-marked fish lost their secondary tag. Estimates of the numbers of tagged fish in each stratum and in the entire river were generated using the corrected counts. A tag abundance curve was drawn as recommended by Tschaplinski and Hyatt (1990) and English et al. (1992) with the resultant line intercepting the x-axis ($t = 0$) at the known number of tags applied. Residence time was calculated by dividing the area under the tag abundance curve by the total number of tags initially applied.

In 1987 at Black Creek, Petersen disks were applied to 68 adult coho at the counting fence 7 d after the first passage of fish. In 1988, 200 adult coho were tagged with spaghetti tags during the first 3 d of significant upstream migration. In 1989, Petersen disks were applied to 102 adult coho on the first day of substantial emigration, and a second group of 72 fish were tagged 19 d later; residence time was the mean of the values calculated for each of the tag groups.

Relatively low fish numbers prevented us from conducting an adequate tagging program in French Creek in 1987. Hence, residence time was determined by means of an iterative estimation procedure, described by Bocking et al. (1988), that incorporated all available information from fence counts and visual survey counts. In 1988, we applied spaghetti tags to groups of 50 and 20 adult coho on the second and third days of substantial upstream migration and combined the data from these two groups to estimate residence time. In 1989, Petersen disks were applied to 15 adult coho on the first day of significant migration, and disks of another colour were applied to 33 fish 16 d later; residence time was the mean of the values calculated for each group.

Jack coho were too small to tag, and therefore, it was not possible to determine their residence time. Hence, their residence time was assumed to be the same as that calculated for adult coho.

Area-Under-the-Curve Escapement Estimation

To estimate escapement, the numbers of fish seen in each 250-m unit were expanded to yield an estimate of the number of live fish in a stream on the *i*th day (p_i):

$$(1) \quad p_i = \sum_{h=1}^{L} N_h \cdot ns_{ih}^{-1} \sum_{j=1}^{ns_{ih}} fo_{ihj} \cdot oe_{ihj}^{-1}$$

where L is the number of strata, N_h is the number of 250-m units in stratum h, ns_{ih} is the number of 250-m units surveyed in stratum h on the ith survey, fo_{ihj} is the number of fish observed during surveys in unit j in stratum h on the ith survey, and oe_{ihj} is the observer efficiency (the fraction of the number of fish present in unit j in stratum h on the ith sampling day that are detected by the surveyor). Observer efficiency can also be a function of the number of fish detected.

The area under each escapement curve (*auc*) was given by

$$(2) \quad auc = 0.5 \cdot \sum_{i=2}^{n} (t_i - t_{i-1}) \cdot (p_i + p_{i-1})$$

where t_i is the number of days since the first fish entered the survey area and n is the number of surveys that fish were seen + 2. The surveys were temporally bounded by the day when the first fish were counted at the fence entering the survey area ($i = 1$, $p_i = 0$) and the first day when it was assumed that there were no longer any live fish in the survey area (t_n where $p_n = 0$). Note that $t_i = 1$ and $p_i = 0$ for the day when the first fish entered each stream and t_n is the number of days that live coho are present in each stream; thus, $p_n = 0$. When fish were still observed on the last survey, the escapement curve was drawn to zero between 5 and 15 d later depending on the condition of fish during the final census and stream conditions.

The area under each escapement curve (*auc*, measured in fish-days) was divided by the estimated residence time (*rt*, measured in days) to yield an escapement estimate.

Cochran (1977) derived the formula used to provide an unbiased estimate of the variance for the stratified random design (his equation 5.12), but it is not possible to estimate the variance around p_i for nonprobability sampling methods (stratified index design). For the SRS, estimates of the variance associated with the area under each escapement curve and the variance of the total escapement estimate were given by

$$(3) \quad V(auc) = 0.25\,[\sum_{i=2}^{n-1} V(p_i)\,(t_{i+1} - t_{i-1})^2]$$

$$(4) \quad V(esc) = V(auc) \cdot rt^{-2}.$$

An implicit assumption of the variance calculations was that the values for *rt* and *oe* were known exactly.

Results

Observer Efficiency

The true number of fish in a stream section was always unknown (i.e. both observed and electrofished counts might be underestimates), and in some cases the number of fish seen by observers was greater than the number of fish detected by electrofishing. However, there was no apparent relationship between fish density and the ratio of the number of fish observed to that electrofished. Sixty-six observer efficiency tests were performed when the number of fish observed was less than six, and 20 when six or more fish were seen. In 15 (22.7%) of the lower density instances and four (20.0%) of the higher density cases, the number of fish seen was greater than the number of fish detected by electrofishing.

There was little statistical basis for separating the data for either the two cohorts or the three years. For instance, the interactions between the age categories and the covariate were never significant ($p > 0.05$); therefore, we never rejected the null hypothesis of no interaction; the assumption of homogeneity of slopes appeared plausible. The interaction between year and covariate was significant only for Black Creek jacks.

When the interactions between the covariate and the treatment were not significant, the power of the tests was low. If the slopes for the regressions were assumed to be parallel, although it was generally not possible to reject the null hypothesis of no difference among intercepts, again the power of the tests performed was very low. For instance, using the example of Black Creek adults and jacks, the power of detecting a difference of two fish was only 0.14 at $\alpha = 0.05$. In our final analysis, we always separated data for the two age classes, and the decision to separate or pool data for the various years was based chiefly on sample sizes.

In 1989, there were sufficient measurements of adult coho observer efficiencies in each system to analyze these data sets on their own (Table 1). Transformations did not improve the fit of the lines, or the fit of the residuals, so linear regressions on the untransformed data were used to describe the 1989 observer efficiency relationships. During 1989, a higher proportion of the adult coho present were seen in Black Creek than in French Creek, except at extremely low densities. In 1987 and 1988, generally fewer observer efficiency tests were performed than in 1989, and the range of fish densities when the tests were performed was restricted. Therefore, for each system, the adult coho data for 1987 and 1988 were pooled with the 1989 data. With these pooled data sets, there generally was increasing variability in the numbers of fish observed at higher densities, and the residuals were found to have a heteroscedastic distribution. To correct for this, the data were logarithmically transformed [ln (number of fish + 1)] and regressions on the transformed data were used. Regardless of fish density, a higher proportion of adults present were seen in Black Creek than in

TABLE 1. Parameters for linear and nonlinear (ln + 1) regressions between the number of coho observed during visual surveys and the maximum of this number and the number seen or captured during electrofishing surveys. *n* is the number of observer efficiency tests performed when at least one fish was seen or captured.

				Linear relationship			Nonlinear relationship			Relationship used	
Creek	Cohort	Year(s)	*n*	Slope	Constant	r^2	Slope	Constant	r^2	Year(s)	Type
Black	Adults	1987	4	1.00	−2.00	0.90	1.16	−0.71	0.69	1987–89	Nonlinear
		1988	8	0.37	3.01	0.58	0.75	0.21	0.87	1987–89	Nonlinear
		1989	10	0.93	−1.00	0.97	1.14	−0.58	0.94	1989	Linear
		1987–89	22	0.73	0.24	0.78	0.95	−0.18	0.85	—	—
French	Adults	1987	4	1.67	0.50	0.11	1.14	−0.65	0.73	1987–89	Nonlinear
		1988	16	0.34	0.73	0.67	0.75	−0.20	0.48	1987–89	Nonlinear
		1989	14	0.56	0.41	0.87	1.05	−0.48	0.89	1989	Linear
		1987–89	34	0.48	0.36	0.78	0.89	−0.33	0.69	—	—
Black	Jacks	1987	4	0.09	0.74	0.39	0.45	0.02	0.57	1987–89	Linear
		1988	5	−0.50	0.57	0.28	−0.81	2.80	0.28	1987–89	Linear
		1989	6	1.05	−0.46	0.86	1.48	−0.76	0.85	1987–89	Linear
		1987–89	15	0.40	0.98	0.22	0.89	−0.17	0.43	—	—
French	Jacks	1987	1	—	—	—	—	—	—	1987–89	Linear
		1988	4	0.50	−0.50	1.00	1.00	−0.69	1.00	1987–89	Linear
		1989	10	0.86	−0.71	0.94	1.22	−0.76	0.77	1987–89	Linear
		1987–89	15	0.73	−0.65	0.88	1.13	−0.72	0.81	—	—

TABLE 2. Mean annual residence time estimates (d) obtained at Black Creek and French Creek, 1987–89. Estimate for French Creek in 1987 was derived using a recursive estimation procedure described in Bocking et al. (1988). All other estimates were obtained from tagging studies.

	1987	1988	1989
Black Creek	16.6	8.0	15.0
French Creek	13.3	16.7	15.5

TABLE 3. Date on which peak numbers of coho salmon were seen in Black Creek and French Creek during 1987–89 for each sampling design.

Year	Design	Cohort	Black	French
1987	SIS	Adults	30 Nov.	30 Nov.
		Jacks	5 Dec.	30 Nov.
	SRS	Adults	5 Dec.	30 Nov.
		Jacks	5 Dec.	30 Nov.
1988	SIS	Adults	15 Nov.	14 Nov.
		Jacks	15 Nov.	14 Nov.
	SRS	Adults	15 Nov.	14 Nov.
		Jacks	15 Nov.	19 Nov.
1989	SIS	Adults	11 Dec.	30 Nov.
		Jacks	11 Dec.	28 Oct.
	SRS	Adults	18 Dec.	30 Nov.
		Jacks	11 Dec.	13 Nov.

French Creek. For jacks, for each system, data for the three years were pooled and regressions computed on untransformed data (Table 1), since transformations did not improve the distribution of the residuals. When fewer than about four jacks per 250 m of stream were present, a higher proportion of these were seen at Black Creek than at French Creek, while at higher densities, the reverse pattern occurred.

Residence Time

There were no consistent differences in the efficiency of observation for the different colours of tags used to estimate residence time (J. R. Irvine, unpubl. data). There were also no obvious differences in the detectability of tagged and untagged fish. Therefore, in the estimation of residence time, numbers of tagged fish observed were expanded using the same observer efficiency relationships determined for untagged fish.

In 1988, when spaghetti tags were used to determine residence time, tag retention was estimated at 70%; hence, the numbers of tagged fish seen that year were expanded by 1.43. For the other years, when Petersen tags were used, no evidence of tag loss was obtained and these data were not expanded for tag loss. The mean annual estimate of residence time for each system (Table 2) ranged between 13 and 17 d with one exception, that being the estimate for Black Creek during 1988 which was only 8 d.

Escapements

The first significant upstream migration of coho past the counting fences generally coincided with the first major fall freshet. Peak numbers of fish were observed in late November to early December during 1987 and mid-November during 1988 (Table 3). In 1989, fish were observed in each system over a more protracted period than the previous years (Fig. 3), with peak numbers of fish being seen between late November and mid-December.

The timings and durations of runs were usually similar for jack and adult coho. In 1987 and 1988, peak numbers of jack and adult coho were seen on the same date six times out of eight (Table 3). In 1989, a similar pattern existed, although at French Creek, peak numbers of jacks occurred earlier than adults (Fig. 3).

Escapement estimates obtained using SRS and SIS were compared with the minimum known escapement and the three mark–recapture estimates of escapement (Table 4). Escapements estimated by the SRS design were generally low; they were less than the minimum known escapement 10 times out of 12 and were never within the range of the three mark–recapture estimates, although in one instance, they exceeded each of the mark–recapture estimates. The SIS design produced estimates that were generally closer to mark–recapture estimates and were less variable than the SRS, particularly for adult coho.

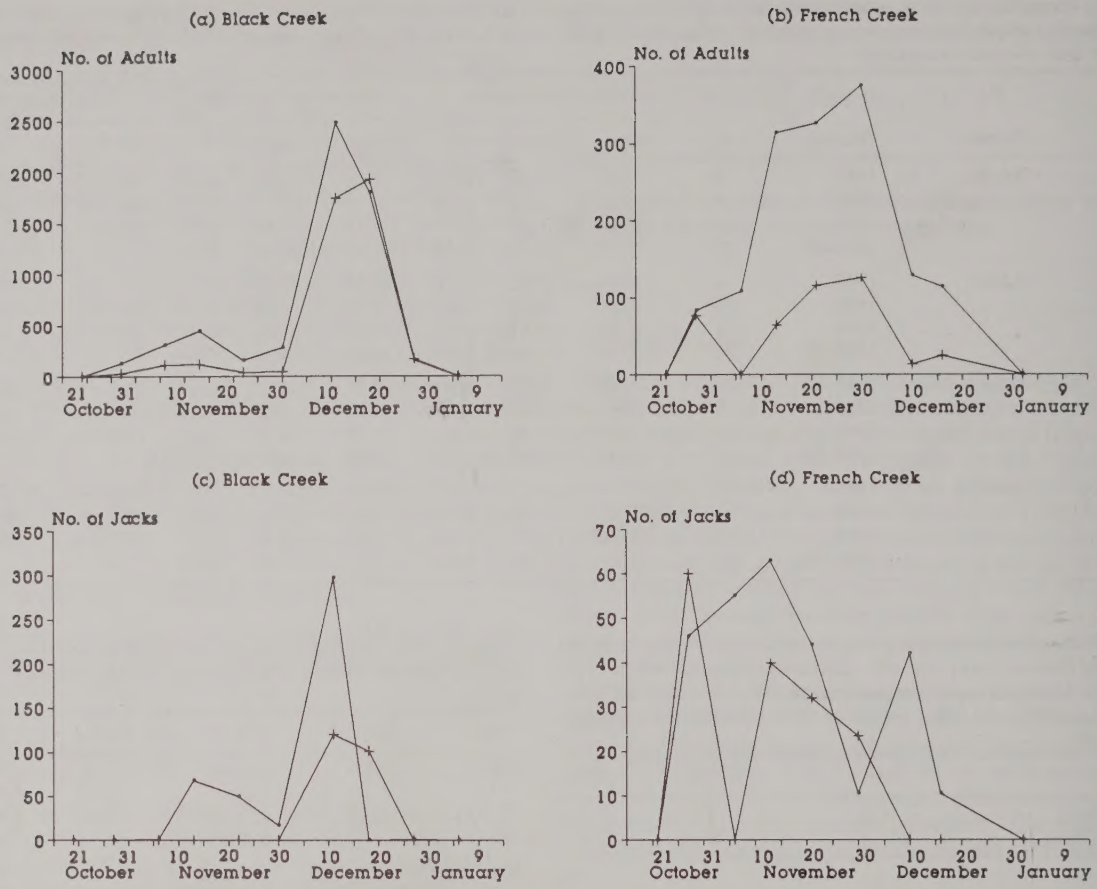

FIG. 3. Estimated numbers of adult and jack coho in Black Creek and French Creek during 1989 using stratified random sampling (SRS, +) and stratified index sampling (SIS, ●). Similar escapement curves were drawn for 1987 and 1988 but are not presented here.

SIS estimates of adult coho were closer than SRS estimates to mark–recapture model estimates in all cases. SIS estimates of jack coho salmon were not as close to mark–recapture jack estimates as SIS estimates of adults were, but they were closer than SRS estimates of jacks five times out of six. With one exception, the coefficients of variation for estimates of the numbers of adult coho were less than for estimates of the numbers of jack coho in the same system and year (Table 4). Variance estimates were themselves highly variable.

Discussion

For each of three years and in two streams with widely varying spawning escapements, estimates of the numbers of adult coho salmon obtained using the area-under-the-curve method and data from visual surveys in stratified index areas (SIS) were similar to independent mark–recapture estimates. In contrast, estimates of adult coho escapements obtained using data from surveys in areas randomly selected within strata (SRS) were more variable and were usually less than the minimum known escapement. Estimates of jack coho using either sampling design were much lower relative to mark–recapture estimates than were estimates of larger adult fish.

Estimates based on data from random sampling are unbiased (Cochran 1977). However, when aggregated populations are randomly sampled, there is a higher probability of sampling low-abundance areas than high-abundance areas, so one would expect a SRS design usually to underestimate the population but occasionally to greatly overestimate it. This is what happened in our study. The distribution of fish was highly aggregated. SRS estimates were less than the minimum known escapement 10 times our of 12, but in one instance the SRS estimate exceeded all the mark–recapture estimates. Our SIS approach ensured that both high- and low-abundance areas were sampled during each survey period and consequently yielded estimates that were similar to the mark–recapture estimates.

There are several likely reasons why indexing estimates for jack coho were considerably less accurate than for adult coho and were almost always underestimates of escapement. We probably overestimated our efficiency of observing jack coho. The smaller size of the jacks made them much more difficult to see or capture than the larger adult coho. Overestimating the efficiency of observing jacks would result in an insufficient expansion of the data and produce a consistent low bias in the escapement estimates for jacks. In addition, we assumed that residence time for jacks was the same as for adults, and this may not be a valid assumption.

Observer efficiency and residence time are important variables in the estimation of escapement using the area-under-the-curve method. In our calculation of escapement estimates, we did not account for the uncertainty associated with our estimates of observer efficiency or residence time. We were therefore not

TABLE 4. Comparison of escapement estimates for Black Creek and French Creek adult and jack coho salmon during 1987–89. The minimum known escapement (marked fish at counting fence plus unmarked fish captured upstream), the escapement estimates obtained using SRS and SIS as well as mark–recapture (MR) estimates obtained using the escapement simulation model, the Bayesian approach, and the Petersen method are given. Variability around the SRS escapement estimates as measured by the coefficient of variation (CV) where *n* is the number of visual surveys conducted is also indicated.

Creek	Cohort	Year	Min.	SRS	(*n*, CV)	SIS	MR	Bayesian	Petersen
Black	Adults	1987	718	330	(5, 0.49)	633	749	790	788
		1988	2122	1101	(7, 0.18)	3179	3122	4083	4059
		1989	2841	2364	(8, 0.35)	3267	3272	3884	3809
French	Adults	1987	67	141	(3, 0.36)	114	107	123	111
		1988	878	411	(6, 0.11)	736	993	1038	1037
		1989	380	231	(7, 0.23)	797	527	679	743
Black	Jacks	1987	536	51	(4, 0.67)	152	730	1072	1020
		1988	174	29	(7, 1.79)	351	343	622	527
		1989	453	126	(8, 0.66)	255	613	1585	1744
French	Jacks	1987	95	98	(3, 0.28)	81	216	212	187
		1988	117	15	(6, 0.54)	61	192	230	216
		1989	182	78	(7, 0.28)	138	241	288	376

able to calculate confidence limits around estimates of escapement that incorporated all the variability around these estimates.

A complex relationship exists between the number of fish in a part of a stream and the number of fish seen by surveyors. Shardlow et al. (1987) found that fish species, observer experience, method of observation, and stream habitat all affected the probability of observing salmon. In our study, we only had one species of fish, although the efficiency of observing the two age classes probably varied. Solazzi (1984) reported that observers saw an average of 76% of the adult coho and 48% of the jack coho present in headwater spawning streams. Shardlow et al. (1987) found that modest amounts of practice reduced the experience effect. All our observers were experienced, and results from a pilot study (Johnston et al. 1987) indicated no significant differences among observers in the numbers of adult coho seen. We deliberately standardized our method of observation. We believe the the length of our individual sampling units (250 m) was sufficient to encompass a diversity of habitats, and we measured observer efficiency over this same length of stream.

In large rivers (Shardlow et al. 1987) and lakes (Pierce et al. 1990), it may be desirable to obtain separate efficiency estimates for specific habitat types. Fish abundance can then be predicted from estimates of the total areas of the habitat types and fish numbers within these habitats (Hankin and Reeves 1988).

Observer efficiency estimates suggest that it was almost always more difficult to see adult coho in French Creek than in Black Creek. Coho in Black Creek tended to aggregate in shallow, narrow areas of the creek where visibility was relatively good. French Creek is generally deeper and faster flowing than Black Creek; hence, visibility was poorer. There is little doubt that observer efficiency may vary in different streams and that observer efficiency should be measured wherever visual surveys are conducted.

Our estimate of residence time for coho in Black Creek during 1988 was lower than during other years. In 1987 and 1989, beaver dams apparently prevented fish from reaching the main spawning areas in the upper Black Creek watershed until early December whereas in 1988, access to this area was possible soon after fish entered the creek. In years when more than one pulse of fish enters a system and these pulses are widely separated in time, it is important to try to collect residence time data separately for each pulse.

The success of using index sites to estimate the total escapement to a particular stream is dependent on how well the sites are selected relative to the distribution of fish in the stream. If only trends in escapements are desired, then visual counts from carefully selected sites can be used as indices of abundance, provided that the abundance of fish in these sites relative to the total abundance in the river is known or does not change drastically from year to year (Beidler and Nickelson 1980). An important longer term goal of our research is to examine the relationship between numbers of salmon in arbitrarily chosen index areas and escapement and whether population estimates in these index areas can be used as reliable indices of escapement.

In this study, we used three techniques to estimate escapement: fish counting fences, mark–recapture, and visual instream indexing surveys. A fish counting fence is perhaps the most accurate way of estimating escapement, as long as the fence can be maintained throughout the period of fish migration (Cousens et al. 1982). We were never able to obtain a complete census of migrating coho salmon in our streams using counting fences. It is beyond the scope of this paper to discuss the relative utility of the three mark–recapture models used. However, particularly with closed mark–recapture models, there are numerous assumptions required to obtain an unbiased estimate (Seber 1982) which are invariably violated when estimating escapement (Cousens et al. 1982; Simpson 1984). Simpson (1984) found that closed model mark–recapture estimates almost always overestimated the true number. Instream indexing may prove to be particularly useful in situations where serious violations of the mark–recapture assumptions are expected and it is not practical to operate a counting fence throughout a fish migration.

Labour costs to estimate escapement utilizing visual survey indexing techniques would typically be less than for these other approaches (Table 5). In general, it took two people a maximum of 2 d to conduct each visual survey in each of our systems. Assuming an average daily cost of $200 per person, the annual cost of conducting visual surveys (SIS or SRS) in our streams was approximately $4000 per stream. While it is desirable to estimate observer efficiency and residence time every

TABLE 5. Approximate annual costs to estimate escapement to a stream like Black Creek assuming a daily cost of $200 per person. Costs for other streams will vary.

	Person-days	Cost ($)
Instream indexing (either SRS or SIS)		
Visual surveys: 2 people × 2 d × 5 surveys	20	4 000
Observer efficiency tests: 4 people × 4 d	16	3 200
Residence time: 2 people × 3 d	6	1 200
Total instream indexing	42	8 400
Mark–recapture		
Surveys: 3 people × 2 d × 5 surveys	30	6 000
Marking: 2 people × 10 d	20	4 000
Total mark–recapture	50	10 000
Counting fence		
Installation: 2 people × 5 d	10	2 000
Operation: 1 person × 60 d plus 2 people × 20 d	100	20 000
Removal: 2 people × 3 d	6	1 200
Total counting fence	116	23 200

year in a system, this may not always be necessary. At Black Creek, it takes approximately an additional 22 person-days to estimate observer efficiency and residence time reasonably well for a total cost of $8400. As a comparison, to estimate escapement in a stream such as Black Creek by mark–recapture requires about 50 person-days annually ($10 000). If a fence or some other location where fish can be captured relatively easily in order to apply marks is not available, the cost may be much higher. To maintain the fish counting fence at Black Creek throughout the fall requires approximately 100 person-days with additional time required to install and remove the fence. In conclusion, although costs may prohibit the use of visual survey indexing techniques to estimate coho escapement on a wide scale, in our view, the method warrants serious consideration for those streams where escapement estimates are required at reasonable cost.

A major disadvantage of the SIS design is the inability to calculate variance estimates. If fish are randomly distributed within strata, selecting index sites is equivalent to selecting a random sample, and variability around index site estimates can be calculated (although these estimates will not include variability associated with residence time or observer efficiency estimates). However, fish do not randomly segregate in our streams. To reduce the likelihood of our estimates being much higher or lower than the actual values, we attempted to include index areas with an abundance of good habitat and index areas that had an abundance of poor habitat within each stratum, a form of within-stratum stratification. Stratification can reduce the variability of estimates. However, because we did not know the distribution of all the good and poor habitat within each stratum, we could not calculate variability. In other situations, it may be possible to stratify an entire watershed into good and poor areas. Then, if fish are randomly distributed within each of these strata, or the investigator is able to select sites randomly within these good and poor strata, variability around the estimates can be calculated.

To summarize, results from this research suggest that visual survey results can yield reasonable estimates of adult salmon escapement when coupled with observer efficiency and residence time estimates. This approach is not the most appropriate for all streams; in many instances, a mark–recapture study may prove to be a better method to estimate escapement. It remains for the investigator to determine the best method for the particular situation. There is little doubt, however, that the quality of escapement estimates obtained by visual surveys can be improved by standardizing estimation procedures.

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A Robust Procedure for Estimating Salmon Escapement based on the Area-Under-the-Curve Method

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English, K. K., R. C. Bocking, and J. R. Irvine. 1992. A robust procedure for estimating salmon escapement based on the area-under-the-curve method. Can. J. Fish. Aquat. Sci. 49: 1982–1989.

Salmon spawning escapements are estimated using the area-under-the-curve (AUC) method by dividing the integral of the escapement curve by the average residence time of fish in the survey area. We present two forms of the basic AUC method which differ in the procedure used to estimate residence time from the observations of tagged fish during stream surveys. AUC estimates based on "observed residence times" were sensitive to variability in survey timing, observer efficiency, and tag detection, while those based on "total residence times" were more robust. For two coastal streams, escapement estimates based on "observed residence times" were between 1.1, and 6.8 times larger than an independent escapement estimate (from fence counts and mark–recapture data), while estimates based on "total residence times" were generally closer to the independent estimate (0.74–1.51 times the estimate, and within 26% six times out of seven). The consistency of our results under a wide variety of survey conditions, combined with their strong theoretical basis, indicates that an AUC method based on annual estimates of total residence time and observer efficiency is robust. However, the level of survey effort required for these methods would limit their application to high-priority streams or populations.

On a déterminé l'échappée du saumon à l'aide de la méthode dite de la surface sous la courbe en divisant l'intégrale de la courbe de l'échappée par la durée moyenne du séjour dans la zone du relevé. On présente deux variantes de cette méthode basées sur la procédure utilisée pour estimer la durée du séjour à partir de l'observation de poissons étiquetés lors de relevés de cours d'eau. Les estimations basées sur « la durée du séjour observée » réagissaient à la variabilité du moment du relevé, de l'efficacité des observateurs et de la détection des étiquettes, tandis que celles basées sur « la durée du séjour totale » étainet plus robustes. Dans deux cours d'eau côtiers, les estimations de l'échappée basées sur « la durée du séjour observée » étaient entre 1,1 et 6,8 fois plus élevées qu'une estimation indépendante de l'échappée obtenue à partir de données de marquage et de recapture et de dénombrements à des barrages, tandis que les estimations basées sur « la durée du séjour totale » se rapprochaient beaucoup plus de l'estimation indépendante (de 0,74 à 1,51; soit six fois sur sept dans le cas de 26% des estimations indépendantes). L'uniformité des résultats obtenus lors des divers relevés et la base théorique solide sur lesquels ces résultats reposent indiquent qu'une méthode dite de la surface sous la courbe basée sur des estimations annuelles de la durée du séjour totale et l'efficacité des observateus est robuste. Toutefois, le niveau d'effort en termes de relevés nécessaire à l'application de ces méthodes pourrait limiter leurs applications à des cours d'eau ou à des populations de priorité élevée.

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The area-under-the-curve (AUC) is a method used to convert periodic counts of mature salmon in streams into an estimate of escapement. Escapement is defined as the number of mature salmon that escape marine fisheries and enter the freshwater survey area. The AUC method does not require that all these fish are spawners or that fish are counted during spawning. Despite the wide use and general acceptance of the AUC method, a detailed assessment of the assumptions and problems associated with this escapement procedure has not been published. Ames and Phinney (1977) appear to have been the first to document the application of this method. In their study, point estimates of fish abundance were connected by a contour line to form the escapement curve. Escapement estimates were obtained by dividing the area under the escapement curve by the stream residence time. Ames and Phinney (1977) used the term "residence time" to refer to the average time mature salmon spend in a stream prior to death. Other researchers use "survey life" or "survey area residence time" to refer to the life span of mature salmon in a survey area (Perrin and Irvine 1990; Irvine et al. 1992). The survey area can be the entire stream or only a portion of the stream (e.g. spawning grounds) depending on the survey design. It is important to define the survey area and select the appropriate measure of residence time.

Agencies using the AUC method often focus effort on defining the shape of the escapement curve and assume some constant value for the average time fish spend in the survey area (Pirtle 1977; Beidler and Nickelson 1980; Ames 1984; Johnson and Barrett 1988). This approach assumes that variability in run timing, water flows, and water temperature does not affect the residence time. Recent studies have found that residence time can vary considerably among years for a specific stream, as well as among streams within a year (Bocking et al. 1988; Perrin and Irvine 1990; Irvine et al. 1992). Therefore, whenever possible, AUC escapement estimates should be based on annual stream-specific estimates of residence time.

Studies of coho salmon (*Oncorhynchus kisutch*) escapement from 1987 to 1990 on two streams on the east coast of Vancouver Island have provided information on run timing, population size, in-stream distribution, observer efficiencies, residence time, and field survey constraints (Bocking et al. 1988; Labelle 1990; Irvine et al. 1992). In this paper, we evaluate two forms of the basic AUC method which differ in the procedure used to estimate residence time from observations of tagged fish during stream surveys. Numerical examples are presented to show how within-year variability in survey timing, observer efficiency, and tag detection affects the alternative AUC estimation procedures. In addition, we identify an AUC estimation procedure that has provided reliable estimates of coho salmon escapement and is robust with regard to variability in survey timing and observer effiency.

We recognize that the AUC estimation procedures recommended in this paper require more survey effort than that routinely allocated to each stream within regional escapement monitoring programs. However, it is important that individuals responsible for escapement estimation are aware of procedures that could be implemented on a few streams within each region to provide reliable information on total escapement and stream residence times.

AUC Estimation Procedure

The AUC estimation procedure has two basic components. The first is an estimate of the number of fish-days derived from the area under the escapement curve (*auc*). The escapement curve typically starts at zero fish on day zero, is drawn through a series of point estimates determined from visual surveys, and ends at zero fish at some later date. The second component to the AUC escapement estimate is the residence time (*rt*).

There are two categories of factors that can affect the values estimated for the *auc* and *rt*: (1) those that affect the length of time fish are alive in the stream (e.g. fish maturity, stream discharge, water temperature) and (2) those that affect the surveyor's ability to observe fish (e.g. water depth, water clarity, surveyor experience). Changes in any of these factors will have a similar effect on the *auc* and *rt* estimates. For example, increasing stream temperature might decrease the length of time fish are alive in the stream which would decrease both *auc* and *rt*. In addition to these factors, the definition of the survey area and survey timing can influence both the length of time fish reside in the survey area and the surveyor's ability to observe fish. For example, surveys that cover the whole stream should produce larger estimates for *auc* and *rt* than surveys that cover only the spawning grounds.

By definition, the *auc* estimate integrates the effects of all factors influencing the sequential estimates of the number of fish in a stream into a single estimate of the number of fish-days for the survey area. In contrast, the use of independent estimates of residence time to produce the *auc* estimate may not integrate the effects of all factors and often represent only a small amount of the population surveyed. Accurate estimates of residence times obtained from some tagging or holding experiments may differ substantially from the residence time for fish observed in a survey area. Likewise, residence time estimates derived from the time interval between peak live-to-dead counts may be biased due to sampling error. Perrin and Irvine (1990) reviewed the various methods used to estimate residence time, none of which were believed to provide an unbiased estimate.

Since it is virtually impossible to obtain unbiased estimates of *rt* and *auc*, the pragmatic solution is a method that minimizes the impact of these biases on the AUC escapement estimate. One way to control for biases in *rt* and *auc* is to obtain data required to estimates *rt* from the same portion of the population and to use the same survey techniques used to estimate *auc*. If a portion of the population can be marked as they enter the survey area, *rt* can be estimated from the observation or sighting of marked fish during subsequent surveys (Bocking et al. 1988; Tschaplinski and Hyatt 1990).

Methods

We calculated the in-stream population (escapement) estimate using the following equations. The number of live fish in a stream on the *i*th day (p_i) was estimated by

$$(1)\quad p_i = \sum_{h=1}^{L} fo_{ih}\cdot N_h\cdot ns_{ih}^{-1}\cdot oe_{ih}^{-1}$$

where L is the number of spacial strata (h) within each stream, fo_{ih} is the fish observed during surveys in stratum h on the ith sampling day, N_h is the number of sampling units in stratum h, ns_{ih} is the number of units surveyed in stratum h on the ith sampling day, and oe_{ih} is the observer efficiency (the fraction of the number of fish present in an area that are detected by the surveyor). This equation is slightly simpler than its complement in Irvine et al. (1992) because it does not include the sampling unit subscript "*j*". The resultant sequence of population estimates were combined into an estimate of the area under the escapement curve using

$$(2)\quad auc = 0.5\cdot\sum_{i=2}^{n} (t_i - t_{i-1})\cdot(p_i + p_{i-1})$$

where t_i is the number of days measured from the first day fish enter the survey area to the ith sampling day and $n-2$ is the number of surveys when fish were seen. The surveys are temporally bounded by the day when the first fish enter the survey area ($i=1$ and $p_i=0$) and the last day when there are live fish in the survey area (t_n where $p_n = 0$).

We estimated the tag curves and residence times by first calculating the number of tagged fish alive in the stream on each sampling day (tag_i) using

$$(3)\quad tag_i = \sum_{h=1}^{L} ot_{ih}\cdot N_h\cdot ns_{ih}^{-1}\cdot oe_{ih}^{-1}$$

where ot_{ih} is the number of tagged fish observed alive during surveys in stratum h on the ith sampling day and all other variables are as described above. The area under the tag curve (*auc*) and residence time (*rt*) were estimated using

$$(4)\quad auc_g = 0.5\sum_{i=1}^{n} (t_i - t_{i-1})\cdot(tag_i + tag_{i-1})$$

$$(5)\quad rt = auc_g\cdot rel_g^{-1}$$

where auc_g is the area under the tag curve for a tagged group (g), rel_g is the number of tagged fish in the group released, and rt is the average time that tagged fish remain in the survey area (residence time).

Finally, the AUC escapement estimate was defined as

$$(6) \quad Escapement = auc \cdot rt^{-1}.$$

Two Alternative Forms of AUC Estimation Procedure

The two alternatives forms of the AUC estimation procedure presented in equation 6 are

$$(7) \quad Escapement = auc_o \cdot rt_t^{-1}$$

$$(8) \quad Escapement = auc_o \cdot rt_o^{-1}$$

where auc_o is the area under the observed escapement curve, rt_t is the average residence time estimated from the total tag curve, and rt_o is the average residence time estimated from the observed tag curve.

The terms "observed escapement curve", "observed tag curve", and "total tag curve" are most easily defined through a simple hypothetical example where one pulse of fish enters the survey area and subsequently dies off (Fig. 1). The observed escapement curve assumes that the escapement curve starts at zero fish on day zero ($t = 0$) and ends at zero fish at some later date ($t = n$). Likewise, the observed tag curve assumes that the number of tagged fish present in the survey area on day zero is zero. However, more accurate escapement curves and tag curves can be drawn when we know, with certainty, the number of fish in the survey area on day zero (from fence counts) or the number of marked fish released into the study area. A total escapement curve can be drawn by considering the number of fish enumerated at a fence (or by some other means) on the first day of escapement to be the number of fish in the survey area on day zero ($t = 0$). The other points along the escapement curves are identical for both the total and observed escapement curves. Similarly, the total tag curve is defined when the tagged fish in the survey area on day zero is set equal to the total number of tags applied. In most cases, the initial point is the only difference between the total and observed tag curves. However, further differences occur when the estimated number of tagged fish present in the survey area increases from one survey to the next. Since the total tag curve is a depletion curve, it must be drawn to reflect the maximum number of tagged fish estimated to be alive in the survey area during each survey. The observed tag curve is not a depletion curve but is constructed to reflect the observations of tagged fish, and it must, therefore, be drawn through the point estimates for each survey (see example in Fig. 2). Since the total escapement curve is rarely defined in situations where escapement estimates are obtained from visual surveys, equations 7 and 8 are the only practical forms of equation 6.

Survey Techniques and Tag Curves

The accuracy of the two AUC estimation procedures was assessed using field survey data collected at Black Creek and French Creek from 1987 to 1990. The survey methods were similar in each stream each year (Irvine et al. 1992). The basic approach included foot surveys of a predetermined set of 12

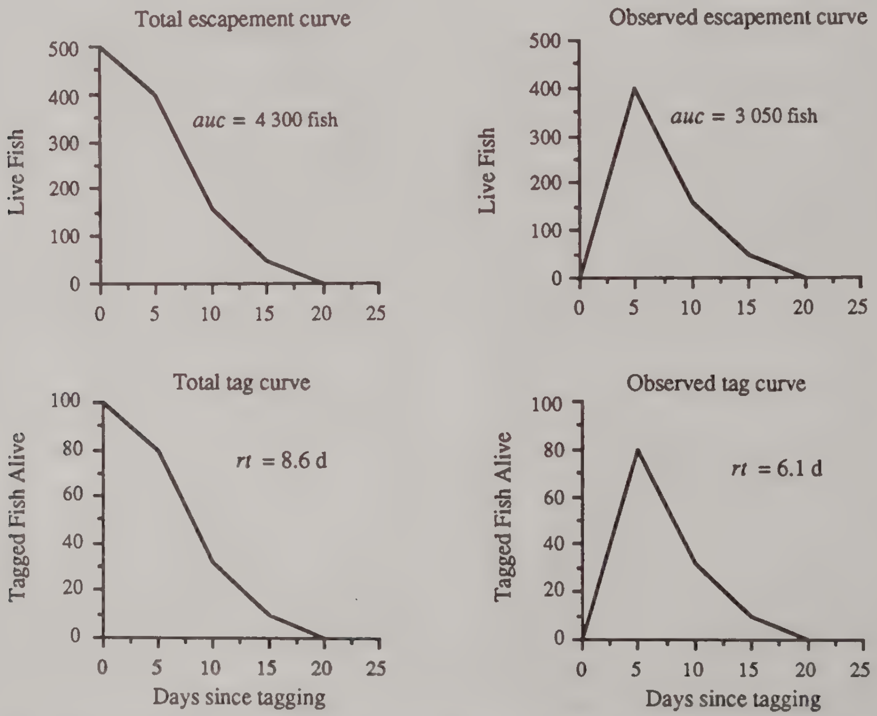

FIG. 1. Hypothetical escapement and tag curves representing the total population and tagged population at times when visual surveys were conducted. Initially, one group of 500 fish entered the stream on day zero, during which 100 members were tagged. The "total" escapement curve represents the actual number of fish alive in a stream in successive 5-day intervals. The "observed" escapement curve is based on expanded survey counts obtained at 5-day intervals, starting on day 5, under ideal conditions (observer efficiency 100%). The corresponding tag curves represent the abundance of tagged fish. Estimates of the area under the escapement curve (*auc*) and residence time (*rt*) are given for each case.

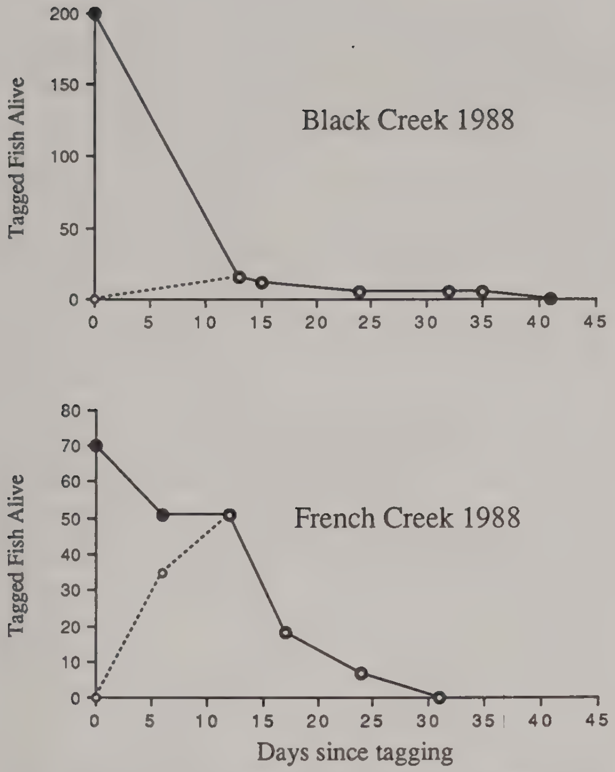

FIG. 2. Selected tag curves based on visual survey data obtained during recent studies on Vancouver Island. Solid and broken lines represent the total and observed tag curves, respectively.

index sites on each stream five to eight times each year. A portion of the fish entering the survey area (48–200 fish) were marked with external tags, and the numbers of marked and unmarked fish observed were recorded during the foot surveys. Examples of total and observed tag curves (Fig. 2) were selected from the available data for Black Creek and French Creek to illustrate some of the characteristics and problems associated with estimating residence time from tag observation data. In 1988, only a few tagged fish were observed in Black Creek, in part due to the relatively long time period between tagging and sighting (13 d). As a result, residence time estimated from the observed tag curve was substantially shorter than the total residence time. Tagged fish were observed during four surveys at French Creek in 1988, but fewer fish were observed during the first survey than during the second (Fig. 2). In this case, the total tag curve was drawn to reflect that the fish observed alive during the second survey must have been alive when the first survey was conducted. In each case, the observed tag curve was drawn through the point estimates for each survey day.

Effects of Survey Timing

The sensitivity of the alternative AUC estimates to variation in survey timing was examined using a hypothetical case in which three pulses of 500 fish enter a steam during successive 5-day intervals, starting with an initial pulse on day 0. Assuming an observer efficiency of 100% in each case (i.e. all fish are detected by the observers) and equal mortality rates for each pulse of fish, three escapement curves (A, B, C, Fig. 3) were drawn based on different time lags between the entry of each pulse of fish and subsequent stream surveys. In case A, each pulse of fish was surveyed (observed) on the date of entry and then surveyed every five days. Here, each pulse of fish is described by a total escapement curve. Although rarely observed in practice, we include this case for illustrative purposes. For case B, the first pulse of fish was not observed until 5 d after the date of entry (an observed escapement curve), but each additional pulse of fish was observed on the date of entry (total escapement curves). Hence, case B is essentially a hybrid of total escapement curves and observed escapement curves for the different pulses. For case C, the first observation of each pulse of fish was 5 d after its date of entry into the survey area, and surveys continued every 5 d thereafter (observed escapement curves). Since we know the mortality rates, we can calculate the two residence times (rt_t and rt_o) that would be computed if only the first pulse of fish was tagged. The combination of these two residence times with the *auc* values for the three escapement curves yields six population estimates that were used to demonstrate characteristics of the alternative AUC estimation procedures.

Results and Discussion

Residence Time and AUC Escapement Estimates

The implementation of the above AUC methods requires the application of a sufficient number of tags to ensure the observation of tagged fish during stream surveys. Ideally, a portion of each major pulse of fish entering the survey area should be tagged. In seven of our eight studies on two streams, we were able to apply an adequate number of tags at least once during the upstream migration period. Extremely low numbers of fish (total return of 107 adult coho) prevented us from conducting an adequate tagging program in 1987 on French Creek. There were three instances where our in-stream observations of two distinct groups of tagged fish were sufficient to compute two estimates of *rt* for the same stream in a single year. In each case the residence time estimated for the first segment of the run was longer than that estimated for pulses of fish entering the stream later in the season. In 1990, the estimated residence time for the first segment of the run entering Black Creek was substantially greater (21.3 d) than that for a later segment of the run (8.6 d). The differences in other years were less (17.9 and 13.1 d for French Creek in 1989, 18.8 and 11.2 d for Black Creek in 1989). Within-year variability in residence time is likely to occur whenever the length of time fish hold in waters adjacent to the survey area is substantially different for different segments of the run. Therefore, estimates of residence time derived from tagging only one portion of the run could result in seriously biased escapement estimates.

Escapements estimates obtained using our two AUC estimation procedures were compared with an independent estimate of population size derived from fence counts and extensive mark–recapture data (Table 1). Escapement estimates based on the observed residence time (equation 8) were between 1.1 and 6.8 times larger than the independent escapement estimate, while escapement estimates based on total residence time (equation 7) were generally closer to the independent estimate (0.74–1.51), and within 26% of the independent estimate six times out of seven. The factor that appears to explain most differences between these alternative AUC estimates is the interval between tagging and the first stream survey (Table 1). The largest differences between the AUC estimates occurred when this interval exceeded 10 d. The portion of the tags applied that were observed during the stream

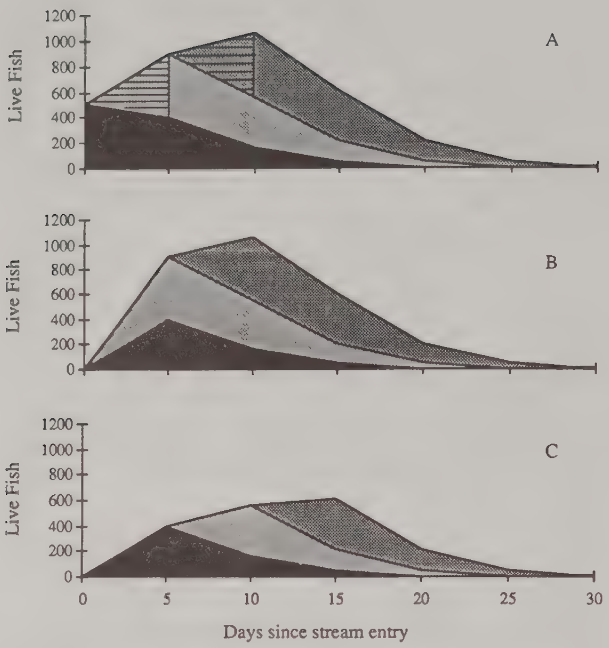

FIG. 3. Examples of three escapement curves based on different survey periods. For each case, three groups of 500 fish were assumed to enter at 5-day intervals, starting on day 0, and dying at a rate described in Fig. 1. The abundance of each group is represented by different shading, and the sum of the shaded areas on each graph is the *auc*. The time lag between fish entry and the first sighting differs for each case: (A) no lag time for each group, (B) a 5-day lag time for the first group and no lag time for subsequent groups, and (C) a 5-day lag time for each group. The hatched area in A represents the surface area that would not have been obtained if surveys had been conducted each day.

surveys (tag detection) is also very important. Tag detection is a function of observer efficiency, survey effort, stream length, and number of tags applied. These factors are discussed below.

Effects of Survey Timing on the Alternative AUC Estimates

Escapement estimates based on curves A and B in Fig. 3 (no lag time between tagging and observing each group, and a 5-day lag for the first group and no lag for later groups, respectively) exceeded the number of fish present when either tag curve was used to determine residence time (Table 2). This occurs because the escapement curves were drawn according to the standard procedure, which requires that the contour line joins each point estimate. As shown for case A, the resultant *auc* exceeds the *auc* that would have been obtained if visual surveys had been conducted daily. This example highlights a potential positive bias in the AUC estimation method caused by the procedure used to draw the contour lines. This type of bias would be substantially reduced if surveys were conducted just prior to each pulse of fish entering the survey area.

Escapement curves based on visual survey data rarely conform exactly to any of the three cases we examined (Fig. 3) because surveyors typically are not able to observe each run segment on the day that the fish enter the stream and because there is usually not a consistent time lag between the date of stream entry and first sighting. The escapement curves generated during our investigations (Irvine et al. 1992) lay somewhere between cases B and C because hydraulic conditions usually prevented field crews from conducting surveys during the 1- to 5-d period after the first group of fish entered the stream, although other segments of the run were observed within 5-d of stream entry. Escapement estimates obtained under such conditions may be biased to some extent, depending on the type of tag curve used to estimate residence time. If the escapement curve is a mixture of cases B and C, escapement estimates based on the observed tag curve will exceed the actual value (possibly by as much as 55%). By contrast, escapement estimates based on the total tag curve tend to be less biased (Table 2). These biases are similar, but less extreme, when the number of fish in each of the groups entering the stream declines over time (Table 3). Therefore, when the lag time between fish entry and the first survey date is not consistent for each segment of the population, the total tag curve should be used to estimate residence time. When a similar lag time exists for each segment of the population (case C), the observed tag curve (equation 8) will provide a more accurate escapement estimate.

A major disadvantage of using the observed tag curve is that it is sensitive to the length of the interval between tagging and the first survey date (Table 4). Estimates based on either total or observed tag curves are comparable if tagged fish are detected soon after tagging, but as the time interval increases, residence time estimates from observed tag curves decrease steadily, while estimates from total tag curves remain consistently higher and deviate little from the true value.

There are other situations where the observed tag curve may be preferable. Our analyses revealed that when a large fraction of the population is tagged, and the first sighting occurs after the period of peak abundance, escapement estimates based on

TABLE 1. Comparison of adult coho escapement estimates (Esc) based on total tag curves (TTC) and observed tag curves (OTC), with an independent mark–recapture (MR) estimate of total escapement (1987–89 data from Irvine et al. 1992; 1990 data unpublished).

				Estimation method						
				Total tag curve		Observed tag curve		Esc/MR		Interval between tagging and first recovery
Stream	Year	MR estimate	*auc*	*rt*	Esc	*rt*	Esc	TTC	OTC	(d)
Black Creek	1987	749	10 508	16.6	633	10.6	991	0.85	1.32	7
	1988	3122	25 432	8.0	3179	1.2	21 193	1.02	6.79	13
	1989	3272	49 005	15.0	3267	10.6	4 623	1.00	1.41	7
	1990	1237	18 075	15.0	1205	7.2	2 510	0.97	2.03	11
French Ck.	1988	993	12 291	16.7	736	11.1	1 107	0.74	1.12	6
	1989	527	12 354	15.5	797	11.0	1 123	1.51	2.13	3
	1990	228	5 725	20.3	282	16.3	351	1.24	1.54	8

TABLE 2. Comparison of escapement estimates obtained from three types of escapement curves (Fig. 3) where the actual population (Pop) was 1500 fish and fish entered the stream in three equal groups of 500 fish. The total tag curve residence time was 8.6 d and the observed tag curve residence time was 6.1 d.

Escapement curve	Area under the escapement curve (fish-days)	Estimation method: Total tag curve		Estimation method: Observed tag curve	
		Escapement	ESc/Pop	Escapement	Esc/Pop
A	15 370	1787	1.19	2520	1.68
B	14 120	1642	1.09	2315	1.54
C	9 120	1060	0.71	1495	1.00

TABLE 3. Comparison of escapement estimates obtained from three types of escapment curves (Fig. 3) where the actual population (Pop) was 1500 fish and fish entered the stream in three groups of decreasing numbers (900, 450, and 150 fish). The total tag curve residence time was 8.6 d and the observed tag curve residence time was 6.1 d.

Escapement curve	Area under the escapement curve (fish-days)	Estimation method: Total tag curve		Estimation method: Observed tag curve	
		Escapement	ESc/Pop	Escapement	Esc/Pop
A	14 370	1671	1.11	2356	1.57
B	12 120	1409	0.94	1987	1.32
C	9 120	1060	0.71	1495	1.00

TABLE 4. Comparison of residence time estimates obtained under different time intervals between tagging and first stream survey. All estimates are based on the tag curves of Fig. 1.

Time interval (d)	Residence time (d): Total tag curve	Residence time (d): Observed tag curve
1	8.0	7.5
2	8.2	7.2
3	8.3	6.8
4	8.5	6.5
5	8.6	6.1
6	8.4	5.4
7	8.3	4.8
8	8.2	4.2
9	8.1	3.6
10	7.9	2.9
11	8.1	2.5
12	8.2	2.1
13	8.3	1.8
14	8.4	1.4

the total tag curve are negatively biased, but those based on the observed tag curve are only slightly positively biased.

Effects of Observer Efficiency on the AUC Estimates

One of the most significant differences between the two AUC equations is the effect observer efficiency has on the escapement estimate. In equation 7, the observer efficiency affects all the data points used to estimate auc_o and rt_t, except the first point on the total tag curve (the y-intercept). This first point is the known number of tags released into the survey area and therefore is not affected by observer efficiency. Consequently, observer efficiency must be estimated so each of the survey observations can be expanded to represent the total number of fish in the survey area on that date. AUC estimates based on the observed tag curve (equation 8) will be less sensitive to changes in observer efficiency than those based on the total tag curve because the observer efficiency affects all the data points used to estimate the auc_o and rt_o. In fact, an estimate of observer efficiency is not required if (1) tags are applied and observed throughout the escapement period and (2) tagged and untagged fish are equally detectable. Under these conditions, the same observer efficiency expansion factors are applied in the numerator and denominator of the AUC equation and therefore cancel. Unfortunately, these conditions are difficult to fulfill. Despite substantial tagging efforts on each stream each year, we were never able to apply a sufficient number of tags to ensure that tagged fish were observed during each survey period.

Since AUC estimates based on total tag curves require an independent estimate of observer efficiency, it is important to assess the sensitivity of these estimates to uncertainty in observer efficiency. When total tag curves are based on the numbers of tagged fish observed during the same surveys used to define the escapement curve, changes in observer efficiency will have a greater effect on the area under the escapement curves than on the residence time estimate (Fig. 4). A fourfold increase in observer efficiency (0.2–0.8) causes a corresponding decrease in the *auc* but only a twofold decrease in total residence time (rt_t). Figure 4 also reveals that each incremental increase in observer efficiency does not translate into a proportional decrease in escapement estimates. Errors in the estimation of observer efficiencies will have a larger effect on the escapement estimate when the actual observer efficiency is low (< 0.4) than when it is high (>0.4). Fortunately, observer efficiencies exceeding this level are often obtained while conducting visual surveys of coho escapements in small coastal streams (Solazzi 1984; Johnston et al. 1987; Bocking et al. 1988). If the tagged and untagged fish are equally detectable, and observer efficiency is measured under the same conditions as encountered during the surveys, p_i and tag_i can be based on a common set of observer efficiencies. This approach will min-

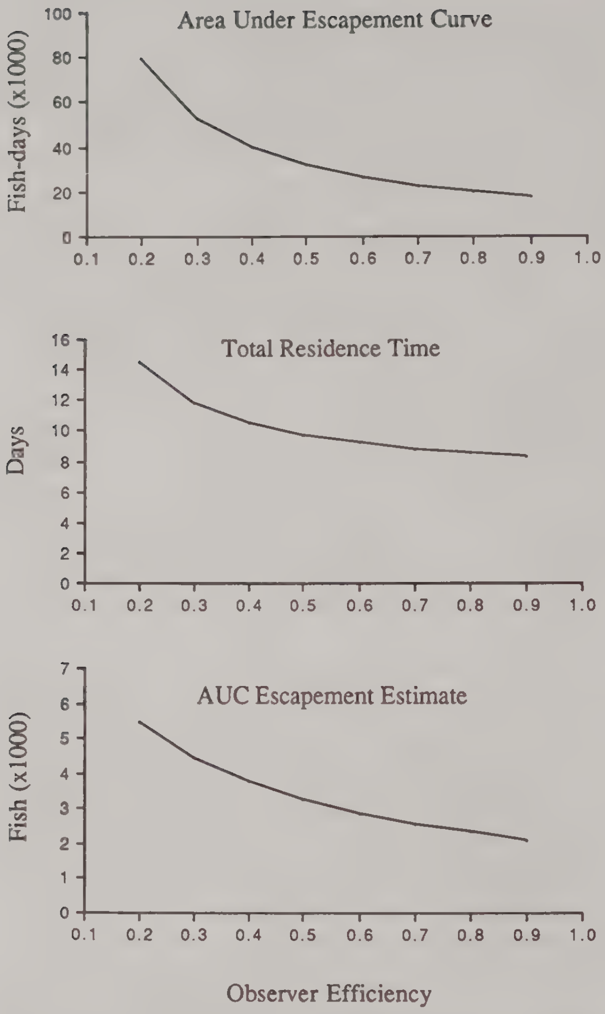

FIG. 4. Effects of different observer efficiencies on each component of the escapement estimates. This example is based on visual survey data collected from Black Creek in 1988 (source: Irvine et al. 1992).

imize the sensitivity of the escapement estimates to errors in the observer efficiency estimates.

Effects of Tag Detection on the Alternative AUC Estimates

The probability of not seeing a tagged fish in an area when it is present may be estimated using information on the size of the study area and a preliminary estimate of observer efficiency. For our Black Creek and French Creek studies, the total sampling area was subdivided into six strata and about 100 sampling units, and usually two sampling units (each 250 m in length) were surveyed per stratum during each census (Irvine et al. 1992). Given an average observer efficiency of approximately 50%, the probability (P) of not seeing any tagged fish in a sampling unit is given by $P = 0.5^{dn}$ where d is the density of tagged fish in the survey area and n is the number of sample units surveyed. The higher the probability, the more likely the estimated residence time will be negatively biased. Using this model, the effect of variability in tagging effort and the time interval between tagging and sighting upon the residence time estimate can be assessed under conditions encountered during our study. Assuming that the total tag curve (from Fig. 1) represents the actual die-off pattern, and that tagged and untagged fish are equally detectable, the potential for a negative bias is high (>40%) when fewer than 200 tags are applied and surveys are not conducted within a 6- to 10-day period after marking (Fig. 5). Additional simulations indicated that the magnitude of negative bias was more severe under similar conditions when a smaller estimate of total residence time was used (<8.6 d).

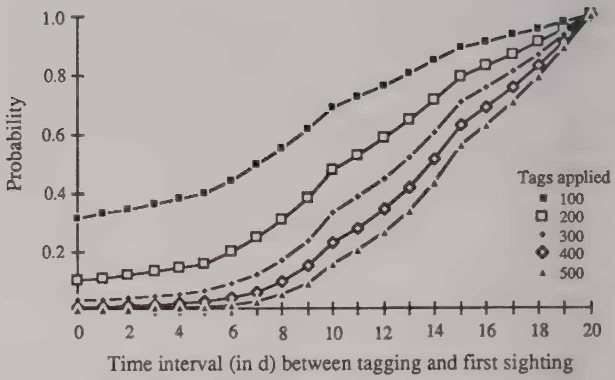

FIG. 5. Probability of not detecting a tagged fish in a given stratum in relation to tagging effort and the time interval between tagging and subsequent sighting. In this example, the observer efficiency is 0.5, the number of sample units in the survey area is 100, the number of units sampled per stratum is 2, and the tagged fish die according to the total tag life curve shown in Fig. 1 (total residence time = 8.6 d).

TABLE 5. Effect of tag detectability on the residence time (*rt*) estimates using different tag curves. Estimates of residence time were obtained by applying the probability levels to the survey counts used to construct the total and observed tag curves in Fig. 1.

Probability of not detecting tag	Total tag curve		Observed tag curve	
	rt	*rt*/8.6	*rt*	*rt*/6.1
0	8.6	1.00	6.1	1.00
0.1	8.0	0.93	5.5	0.90
0.2	7.4	0.86	4.9	0.80
0.3	6.7	0.78	4.3	0.70
0.4	6.2	0.72	3.7	0.61

To assess the impact of P on the alternative residence time estimates, five different levels of tag detection were combined with the hypothetical survey data used to construct Fig. 1. Estimates of rt_t were slightly less sensitive to the probability of not detecting tags than estimates of rt_o (Table 5). Even when there was a 40% chance of not detecting tags, residence time estimates based on total tag curves were still larger than those based on observed tag curves obtained under ideal conditions. A 40% chance of error can occur when dn is reduced to 1.3 fish per area surveyed and the average efficiency is 50%.

This type of detection bias may also affect estimates used to define the escapement curve. The surveyor's ability to obtain an accurate estimate for the peak abundance period is crucial, since these estimates are a major determinant of *auc*. The potential for significant bias in the *auc* estimate is low (<10%) in years when the peak density exceeds two fish per 250 m and at least 500 m are surveyed in each stratum during the period of peak abundance. In streams like Black Creek and French Creek, densities of two fish per 250 m are obtained when there are approximately 200 live fish in the stream. The only case when this condition was not met in our studies was at French Creek in 1987, when the peak abundance was less than 107 fish in the entire stream (Irvine et al. 1992).

Conclusions

The strength of any escapement estimation procedure lies in its ability to detect and compensate for spatial and temporal variability in biological factors, physical factors, and survey conditions. Without annual estimates of residence time and observer efficiency, the AUC method is vulnerable to all factors that affect a surveyor's ability to count fish. The analytical procedures used to combine survey counts with residence time estimates are also important. AUC estimates based on observed residence times can be very sensitive to variability in survey timing, observer efficiency, and tag detection, while those based on total residence times are more robust.

Our four years of research on two streams have included surveys under a wide variety of conditions, in diverse habitats, to assess coho salmon populations that have varied from 100 to 3300 fish. The AUC method based on observed escapement curves and total tag curves (equation 7) has provided reliable escapement estimates for each stream every year. The consistency of our results under a wide variety of survey conditions combined with the strong theoretical basis for our findings supports the conclusion that the method is robust. The method does, however, require that the surveyors meet some minimum level of survey effort. In our study, this included surveying roughly 12% of the stream at least three times each year, Petersen tagging 50–200 fish, and obtaining about 10 estimates of observer efficiency annually. While this level of effort appears to have been adequate to assess coho escapements for streams 20–30 km long with 200–3300 fish, our current data are not sufficient to estimate the levels of effort required to successfully apply these techniques to larger coho populations, longer streams, or other salmon species.

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Size-Dependent Density of the Demersal Fish off Namibia: Patterns within and among Species

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The density of the 40 most abundant demersal fish species off Namibia is inversely scaled to their average length, similar to the scaling of mortality to fish length. However, the density of individual fish species is, on average, scaled to the -2 power of average fish length in the aggregates, indicating that biomass increases (slope > -3) during the growth of most species examined. These findings indicate that size structure of these fish populations is primarily determined by mortality.

La densité des 40 espèces de poissons démersaux les plus abondants sur les côtes de Namibie est inversement proportionnelle à leur longueur moyenne, tout comme le rapport de la mortalité à la longueur du poisson. Toutefois, la densité des espèces prises individuellement est en moyenne proportionnelle à la puissance -2 de la longueur moyenne des poissons dans les groupements, ce qui indique que la biomasse augmente (pente > -3) pendant la croissance chez la plupart des espèces examinées. Ces résultats indiquent que la structure par taille de ces populations de poissons est avant tout déterminée par la mortalité.

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Recent findings have shown that the density of hake (*Merluccius* spp.) in Namibian waters declines with increasing fish length (Gordoa and Duarte 1991). The reduction in fish density with increasing fish size observed for hake is also expected to apply to other fish species in the community, both among and within species. The expectation that the average density of the different fish species present in the community should be negatively scaled to their size derives from the existance of a general negative scaling between organism size and density for both animal and plant populations (Peters 1983; Duarte et al. 1987). A negative scaling of fish density to fish size is also expected within species because (1) distances between neighbor fish are greater in aggregates of large than small fish (Serebrov 1976; Pitcher and Partridge 1979; Pitcher et al. 1985, 1986; Rose and Leggett 1988; Gordoa and Duarte 1991) and (2) mortality should result in positively skewed size distributions at the population level (Persson 1988).

We examine here the scaling of numeric density and size for the 40 dominant demersal fish species off the Namibian coast. We then compare the observed scaling between density and length of individual fish species with the inverse scaling expected if natural mortality were the major factor in their population dynamics (Peterson and Wroblewski 1984; McGurk 1986).

Methods

We used data, derived from trawling surveys, on the density and size (length, centimetres) of the 40 most abundant demersal fish species off Namibia (Table 1). The catch data used in this study were collected during four 20-d cruises, from September 1987 to January 1989, along the continental shelf (100- to 500-m isobaths) of Central and Southern Namibia. Additional details on the length and depth distribution of these species are given in Macpherson and Duarte (1991).

Sampling methods are described in Gordoa and Duarte (1991) and Macpherson and Duarte (1991). Approximately 70 stations were located within the studied area using a stratified random design (Macpherson et al. 1985). Samples of fish were captured during daylight, to avoid vertical migration of the fish (Gordoa and Macpherson 1991), with a commercial stern trawl using bottom nets (two warps, headlines >20 m, heights between 2 and 4 m, 20-mm mesh size in codend). Each station was trawled for 30 min at a speed of 3 kn, thereby sweeping a distance of 1.5 nautical miles and an area of about 3.5 ha. In each trawl set, we measured, for each species, the total number and weight of fish and the total length (centimetres) of all fish collected, or a subsample of 250 when more than 300 were captured. This method should yield adequate estimates of the density (number of fish per square metre) and size distribution (for individuals older than 1 yr) within the swept area for all the species, except *Trachurus trachurus*, which is not confined to a few metres above the bottom as are the other species. Yet, differences in catchability for these species, which are presently unknown, may be responsible for some of the error in our analysis. We refer to each trawl set as a sample and use the term biomass to refer to the weight of fish per unit area.

The extent of aggregation of the fish was characterized by the skewness of the density distribution for each species, positive skewness being indicative of aggregated distributions (cf. Sokal and Rohlf 1969; Gordoa and Duarte 1991). The size dependence of fish density was then examined by testing for significant relationships between the average length and density of the fish, both within and among species. We described the

TABLE 1. Number of trawls (N), geometric mean density, geometric mean size (maximum and minimum), exponential mortality (M) per unit length increase, and constants (intercept a and slope b), and coefficient of determination (R^2) of the regression equation log density = a + b log fish size.

Species	N	Density (no.·m^{-2})	Length (min–max) (cm)	M (cm^{-1})	a	b	R^2
Arnoglossus capensis	12	0.00078	12.2 (13.4–10.1)	0.306	0.77	−3.57	0.08[a]
Austroglossus microlepis	45	0.00010	40.9 (47.0–38.1)	0.058	−0.04	−2.47	0.69
Brama brama	23	0.00008	50.5 (52.7–48.9)	0.048	0.01	−2.43	0.84
Calorhynchus capensis	23	0.00009	54.7 (63.7–50.0)	0.041	−0.06	−2.32	0.84
Chelidonichthys capensis	86	0.00061	34.8 (41.3–29.5)	0.070	0.59	−2.47	0.22
Chelidonycthys quequeti	11	0.00020	24.5 (29.6–21.9)	0.103	−0.13	−2.62	0.83
Chlorophthalmus atlanticus	23	0.00052	12.6 (16.0–13.9)	0.217	0.31	−3.24	0.52
Coelorhynchus coelorhynchus[b]	14	0.00167	5.7 (7.5–4.6)	0.580	−0.11	−3.43	0.48
Coelorynchus fasciatus[b]	157	0.00354	5.9 (10.1–5.1)	0.148	−1.60	−1.08	0.04
Coelorynchus occa[b]	25	0.00056	6.8 (11.0–7.9)	0.219	−1.09	−2.06	0.28
Congiopodus spinifer	17	0.00008	19.9 (23.1–17.3)	0.145	−0.33	−2.91	0.77
Deania profundorum	21	0.00028	64.7 (75.0–58.5)	0.029	−0.07	−1.94	0.49
Ebinania costaecanaria	61	0.00019	14.6 (19.4–12.1)	0.123	−1.49	−1.90	0.25
Epigonus denticulatus	67	0.00073	12.0 (14.5–9.7)	0.140	−1.32	−1.67	0.11
Etmopterus pusillus	21	0.00006	42.8 (44.0–41.5)	0.060	−0.04	−2.58	0.89
Galeus polli	94	0.00090	30.9 (36.3–26.0)	0.062	0.20	−1.90	0.13
Genypterus capensis	98	0.00009	61.5 (73.2–54.7)	0.030	−0.64	−1.89	0.47
Helicolenus dactylopterus	129	0.00106	16.7 (24.4–11.6)	0.098	−0.90	−1.69	0.12
Holohalaelurus regani	47	0.00023	43.1 (50.4–37.6)	0.050	−0.03	−2.20	0.45
Hoplosthetus cadenati	39	0.00121	13.2 (15.7–10.4)	0.199	−0.01	−2.56	0.25
Japonoconger africanus	22	0.00006	56.9 (63.2–53.3)	0.039	−0.23	−2.25	0.80
Lepidopus caudatus	72	0.00033	57.5 (72.0–51.6)	0.020	−1.35	−1.21	0.10
Lophius bomerinus	185	0.00021	42.3 (59.4–32.0)	0.042	−0.66	−1.85	0.28
Malacocephalus laevis[b]	36	0.00056	5.8 (10.6–5.1)	0.298	−1.52	−2.25	0.22
Merluccius capensis	162	0.00690	32.7 (48.6–26.6)	0.073	1.88	−2.68	0.23
Merluccius paradoxus	122	0.00701	31.0 (50.0–22.8)	0.059	0.86	−2.03	0.17
Nezumia aequalis[b]	59	0.00363	4.7 (6.4–3.0)	0.458	−1.04	−2.06	0.09
Nezumia longibarbata[b]	24	0.00080	3.0 (4.0–2.2)	1.372	−1.10	−4.14	0.30
Notacanthus sexspinis	22	0.00009	38.8 (42.5–35.5)	0.062	−0.16	−2.42	0.68
Paracallyonimus costatus	45	0.00054	15.1 (17.6–12.3)	0.159	−0.46	−2.35	0.33
Pterotrisus bellocii	23	0.00013	29.0 (30.9–29.2)	0.067	−0.93	−2.03	0.48
Raja clavata	36	0.00008	59.2 (71.0–51.2)	0.037	−0.13	−2.24	0.72
Raja confundens	62	0.00013	53.7 (63.4–42.5)	0.035	−0.71	−1.83	0.39
Raja leopardus	20	0.00004	51.5 (57.1–48.9)	0.043	−0.49	−2.29	0.86
Selachophidium guentheri	50	0.00052	20.1 (23.6–17.6)	0.114	−0.25	−2.33	0.36
Squalus blainvillei	44	0.00011	46.9 (51.0–44.8)	0.049	−0.22	−2.36	0.48
Squalus megalops	8	0.00010	45.4 (49.8–42.0)	0.052	0.00	−2.37	0.89
Trachurus trachurus	69	0.00023	31.8 (35.6–30.5)	0.045	−1.64	−1.48	0.18
Tripterophycis gilchristi	21	0.00024	16.3 (18.2–16.1)	0.120	−1.16	−2.05	0.54
Zeus capensis	37	0.00049	19.2 (25.8–15.6)	0.079	−1.29	−1.60	0.29

[a] Nonsignificant ($P > 0.05$) fit.

[b] From head to anus.

scaling of fish density (number of fish per square metre) to fish length (centimetres) using the allometric equation

$$\text{Density} = a\ \text{length}^{b}$$

which has been used extensively to describe the size dependence of organism density (Peters 1983; Duarte et al. 1987). This equation was fitted to data using reduced major axis (Till 1974) linear regression analysis of $\log_{10}$-transformed length and density (i.e. $\log_{10}$ density = $\log_{10} a + b \log_{10}$ length) to prevent bias in regression coefficients due to error in the independent and dependent variables (LaBarbera 1989).

Results and Discussion

The average density of fish species within the study area decreased as the −0.97 power of their average length, which was not significantly ($P < 0.05$) different from a slope of −1, which is in agreement with the reported general scaling (Brown and Maurer 1986) of population density to the −0.3 power of organism weight (i.e. $N = L^{-1} = (W^{1/3})^{-1} = W^{-1/3}$). However, hake showed densities 30 times greater than expected from the regression of fish density on length (Fig. 1). This reflects the fact that hake comprise about 90% of the catch of all demersal species (Newman 1977). Why hake are able to attain such high densities compared with other demersal fish species is presently unknown, but may be related to their food, for they feed on myctophids and euphausiids and include an important, often dominant, canibalistic component in their diet (Roel and Macpherson 1988). Yet, the existence of a single, dominant species appears to be common to other areas, where hake and/or cod comprise most of the demersal fish community, as depicted in fisheries statistics (FAO 1989).

Fish density was positively skewed for all of the species examined (Fig. 2), indicating aggregated spatial distributions

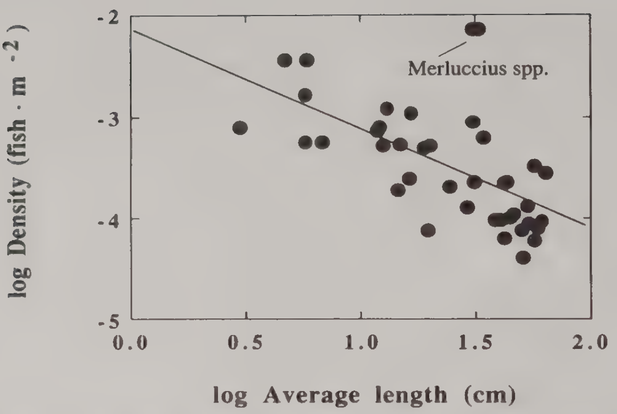

FIG. 1. Relationship between the average areal density of fish and their average length. The solid line represents the fitted regression equation $\log_{10}$ density (fish·m^{-2}) = −2.13 −0.97 $\log_{10}$ length (cm) (R^2 = 0.35, N = 40, $P < 0.001$).

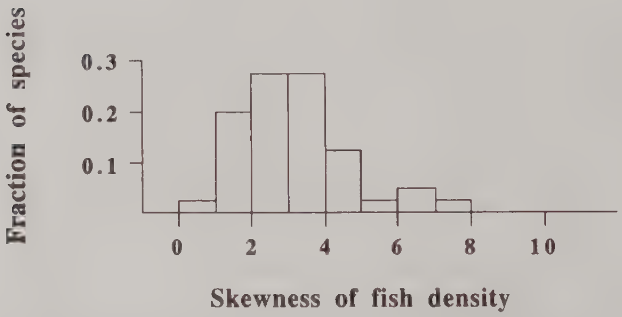

FIG. 2. Frequency distribution of skewness for the distributions of fish density for the different species examined.

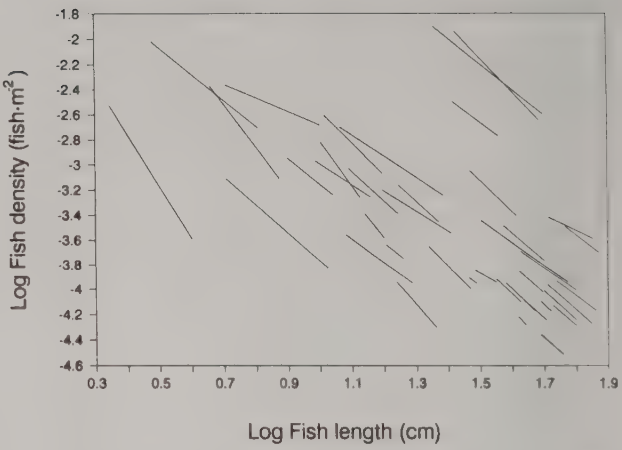

FIG. 3. Relationship between the areal density and the average length in each sample of fish species. Solid lines represent the fitted regression equation for each of the species (Table 1).

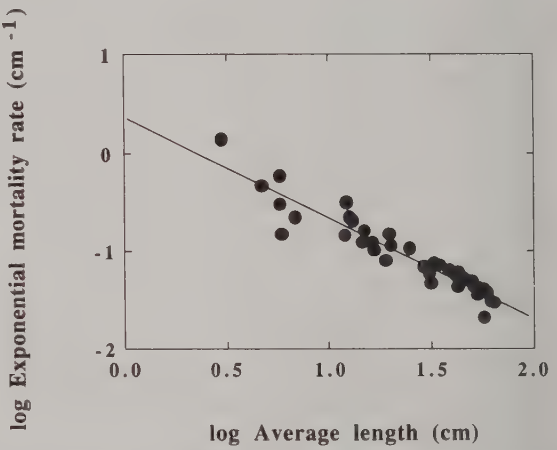

FIG. 4. Relationship between exponential mortality per unit length and the average size of the different fish species examined. The solid line represents the fitted regression equation.

(Gordoa and Duarte 1991). Moreover, we found that aggregates of most fish species consisted of individuals of similar length, as indicated by significant ($P < 0.01$) positive relationships between the average length of the fish and their minimum and maximum length in the sample (Gordoa and Duarte 1991) for all but one species examined, *Arnoglossus capensis* (Table 1). These observations suggest that our finding that hake form aggregates of fish segregated by size (Gordoa and Duarte 1991) is also applicable to most other demersal species off Namibia, as expected from their general increase in size with depth (Macpherson and Duarte 1991).

The density distributions of the individual species across the study area are, in part, dependent on their biogeographical distribution (Mas-Riera et al. 1990). In addition to these biogeographical patterns, we found that differences in average fish length accounted for a significant fraction of the differences in the density of the individual species across the study area (Fig. 3). This was reflected in a general trend, significant ($P < 0.05$) for all species except *A. capensis*, for fish density to decrease as the −2 power of the average fish length (Table 1; Fig. 3). The average slope of −2.27 ± 0.095 (mean ± SE) found here indicates that the biomass of the demersal fish examined increases as fish length increases. Variability of the slope is ecologically relevant, for 10% of the species had slopes steeper than −3, which indicates species that show reduced biomass with increasing fish length (i.e. biomass $\approx$ length^3·density $\approx$ length^3·length$^{<-3}$ $\approx$ length$^{<0}$), reflecting noncompensatory growth. However, 90% of the species had slopes shallower than −3, indicative of increasing biomass with length (i.e. biomass $\approx$ length^3·density $\approx$ size^3·length$^{>-3}$ $\approx$ length$^{>0}$).

The rate of decline in fish density with increasing length should be dependent on the average rate of mortality of the population. Thus, we used the changes in fish density (N) with increasing length (L) to calculate exponential mortality per unit length (M, per centimetre) by fitting the equation

$$M = (\ln N_{L_{\min}} - \ln N_{L_{\max}})/(L_{\max} - L_{\min})$$

to the density and length data for each species (Table 1). These estimates of mortality rate were negatively correlated with the average size of each species (Fig. 4), as described by the equation

$$\log_{10} M\,(\mathrm{cm}^{-1}) = 0.37 - 1.03 \log_{10} \text{average length (cm)}$$
$$(R^2 = 0.89,\ \mathrm{SE}_{\mathrm{slope}} = 0.05,\ P < 0.0001)$$

which indicates that fish mortality is scaled to the inverse of their average length, or as the −1/3 of their average weight

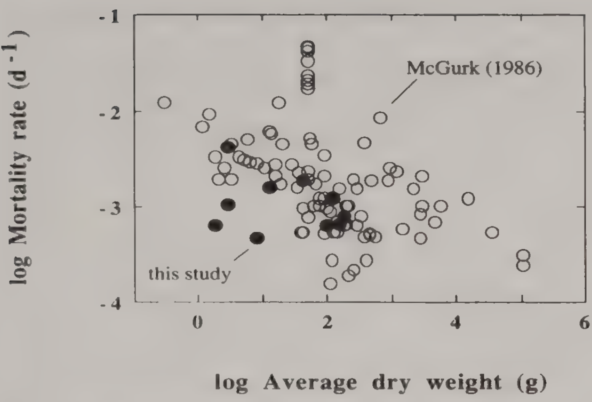

FIG. 5. Relationship between mortality and average dry weight of fish species. Solid circles represent the values estimated here, and open circles represent the data on juvenile and adult fish compiled by McGurk (1986). Dry weight was calculated as 20% of the ratio of biomass and numbers in each trawl.

(i.e. $W \approx L^3$). This estimate of the slope is quite close to, but slightly higher than, the -0.25 slope that described the scaling of mortality to weight for a broad assemblage of fish, mostly pelagic, species (Peterson and Wroblewski 1984; McGurk 1986). The similarity in the scaling of the exponential mortality per unit length to fish size with previous estimates of the scaling of natural mortality to fish size (Peterson and Wroblewski 1984; McGurk 1986) suggests that the size dependence of the density of the demersal fish populations examined here could be accounted for by size-dependent mortality.

Because the exponential mortality per unit length that we estimated cannot be readily compared with other estimates based on time units, we recalculated the exponential mortality rates into time units using estimates of the average growth rates available for some of the species examined (Botha 1971; Morales 1980, 1982; Griffiths and Hecht 1986; Lombarte and Morales 1989; Hecht 1990; Japp 1990, B. Molí, ICM, Barcelona, pers. comm.). Comparison of these estimates, based on density–weight relationships, with data compiled by McGurk (1986) shows them to be within the range previously reported for other fish species of similar size (Fig. 5).

In summary, our findings indicate that the average density of the main demersal fish species off Namibia is size dependent among and within species. The average density of fish is inversely scaled to their average length, similar to the scaling between natural mortality rates and fish size, and in agreement with general descriptions of the size dependence of organism density (Brown and Maurer 1986). The negative scaling of fish density to fish size also holds within species, for we found fish density to change, on the average, as the -2 power of their average size. The scaling of fish density to fish length indicated that biomass increases (slope > -3) during the growth of 90% of the species examined. Thus, examination of the scaling of fish density to fish size may validate theoretical expectations for the mortality of demersal fish species.

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Ranking of Feeding Positions by Drift-Feeding Arctic Grayling (*Thymallus arcticus*) in Dominance Hierarchies

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Hughes, N. F. 1992. Ranking of feeding positions by drift-feeding Arctic grayling (*Thymallus arcticus*) in dominance hierarchies. Can. J. Fish. Aquat. Sci. 49: 1994–1998.

Field experiments in the pools of a mountain stream demonstrate that Arctic grayling (*Thymallus arcticus*) rank feeding positions according to desirability and that competition sorts fish so that the dominance rank of each individual matches the rank desirability of its position. Groups containing the same number of fish always occupied the same set of positions, and positions were added (in reverse order of desirability) as group size was increased; these results show that fish ranked positions. There was an almost perfect correlation between the dominance rank (measured as fish length) of each fish and the rank desirability of its position, suggesting that competition sorts fish among positions. This conclusion was strengthened by the results of sequential removal experiments in which the dominant fish was removed at the end of each day. After each removal the remaining fish almost always moved into the positions previously occupied by fish immediately above them in the dominance hierarchy.

Des expériences sur le terrain menées dans des fosses d'un torrent ont révélé que l'ombre arctique (*Thymallus arcticus*) classe ses positions lors de l'alimentation selon leurs caractères désirables et que la compétition établit l'ordre des poissons de façon à ce que le niveau de dominance de chaque individu correspond au caractère désirable de sa position. Les groupes comprenant le même nombre de poissons ont toujours occupé la même série de positions, et des positions ont été ajoutées (en ordre inverse du caractère désirable) lorsque la taille du groupe augmentait. Ces résultats révèlent que les poissons classent les positions. Il y avait une corrélation presque parfaite entre le niveau de dominance (mesuré comme la longueur du poisson) de chaque poisson et le caractère désirable du niveau de sa position, portant à croire que la compétition établit l'ordre de dominance des poissons selon leurs positions. Cette conclusion a été étayée par les résultats d'expériences séquentielles d'élimination du poisson dominant à la fin de chaque journée. Après chaque élimination, les poissons qui restaient ont presque toujours occupé la position supérieure ainsi laissée libre.

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Drift-feeding stream salmonids that select feeding positions in order to maximize their net energy intake rate (NEI) should rank the desirability of feeding positions using the same criteria. In addition, competition for profitable positions should sort the members of a dominance hierarchy so that the social rank of each fish corresponds to the rank desirability of its position. This process of ranking and sorting should result in a predictable relationship between the layout of the stream habitat and the distribution pattern of the fish. This is because bottom topography and the pattern of current flow play a large part in determining the potential NEI at available positions (Hughes and Dill 1990; Hughes 1992).

These ideas, first expressed by Newman (1956) and supported by Vascotto and Morrow (1973), provide an appealing explanation of the processes that determine the distribution pattern of fish in a dominance hierarchy; however, they have been challenged by other field studies. In fact, both Jenkins (1969) and Bachman (1984) concluded that sorting of fish among ranked positions was not important in determining fish distribution patterns. This is despite the fact that Jenkins found brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) ranked one position as more desirable than all the alternative positions and that the dominant fish in the hierarchy occupied and defended this position. Laboratory studies such as those by Chapman (1962) and Fausch (1984) have been more supportive of Newman's ideas. For example, Fausch showed that the dominance rank of juvenile coho salmon (*Oncorhynchus kisutch*) was closely correlated with predicted NEI at their positions and with growth rate. This result is consistent with the hypothesis that fish are sorting themselves among positions ranked on the basis of NEI.

In this work I describe field experiments which test Newman's hypothesis that fish rank the desirability of feeding positions and the closely related hypothesis that competition sorts fish so that the dominance rank of each individual matches the rank desirability of its position. These experiments were conducted in the pools of a mountain stream using Arctic grayling (*Thymallus arcticus*).

If Arctic grayling rank feeding positions according to desirability I expected positions to be occupied in reverse order of desirability as the number of fish in a pool was increased from one to four. It follows that groups containing the same number of fish should use the same set of positions. If these predictions hold true, then the rank desirability of each position can be determined: it is equal to the number of fish that must be added to the pool before that position is occupied.

Further, if competition sorts fish until the dominance rank of each individual matches the rank desirability of its position,

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I expected a one-to-one correspondence between the dominance rank of each fish and the rank desirability of its position. I also expected that when the dominant fish was removed from a pool, each remaining fish would move into the position previously occupied by the fish immediately above it in the dominance hierarchy.

Methods

I conducted position choice experiments in two pools of Twelvemile Creek, a small mountain stream in interior Alaska, during the summer of 1987. Descriptions of Twelvemile Creek and the methods used in position choice experiments involving a single fish are given in Hughes and Dill (1990); only additional techniques and experimental design are described here.

Experimental Techniques

To help identify individuals, I attached a small colored bird band to the front of each fish's dorsal fin. To avoid the possibility of using fish in more than one experiment each fish was also marked with a small upper caudal finclip.

Arctic grayling are a rugged and cooperative fish; minutes after introduction into a pool individuals begin to compete for positions and feed. Excellent accounts of the behavior involved in this competition are given in Vascotto (1970), Vascotto and Morrow (1973), and Kratt and Smith (1979). Dominance relationships are established fairly quickly; in a two-fish group I have seen the process completed in less than 1 h. In four-fish groups it takes longer but usually less than 24 h (pers. obs.). Once dominance relationships are established social interactions are infrequent and the pattern of distribution is quite stable; individuals spend most of the day feeding from a single focal point or alternating between a pair of very similar focal points. I treated clusters of focal points as single positions if they were grouped around a readily identifiable indentation in the streambed and so close together that only one fish at a time would "occupy" the cluster. During data analysis I outlined positions by drawing a rectangle around the focal point, or cluster of focal points, that fish used when at that position.

The rapidity with which dominance relationships are established and the stability of each fish's feeding position make it possible to reliably record the distribution pattern of fish the day after an experimental manipulation. Position choice of each fish was recorded two or three times during the course of a day at intervals of about 6 h. During the course of each observation the focal point and feeding movements of each fish were traced on a scale map of the pool for a total of 4 min. An additional 30–60 min was typically spent in observing the fish. These additional periods of observation served to confirm the stability of the distribution patterns recorded on the map and to identify rarely used positions which a fish only used once or twice, for short periods, during the course of the experiment.

Experimental Design

I used "group size" experiments and "sequential removal" experiments to test the hypothesis that competition sorts fish among ranked positions. Two pools were used for these experiments: Yellow Flower Pool and Bedrock Pool. The lengths of fish used in these experiments and their dominance rank are given in Table 1. The experiments were conducted between 19 July and 20 August. I assumed that the dominance rank of fish in a group was directly related to its length (Kratt and Smith 1979) and to help ensure this I made sure there was a significant difference in length between individuals in each group. Observations of social interactions made during the course of each experiment were used to confirm this assumption, and in only one case was a small fish seen to dominate a larger individual (see Table 1).

TABLE 1. Length (mm) of fish used in group size experiments in Yellow Flower Pool and Bedrock Pool. Fish in each group are listed in order of decreasing dominance rank. The first four-fish group from each pool was also used in the sequential removal experiment; otherwise, no individual was used/observed more than once.

	Yellow Flower Pool	Bedrock Pool
1st solitary fish	240	280
2nd solitary fish	300	240
3rd solitary fish	210	250
4th solitary fish	180	195
1st two-fish group	270	270
	216	230
2nd two-fish group	260	285
	225	220
1st four-fish group	260	285
	225	240
	240[a]	225
	205	195
2nd four-fish group	260	285
	210	230
	180	190
	155	170

[a] This was the only fish observed to be subordinate to an individual smaller than itself.

In the group size experiments, I recorded the distribution pattern adopted by solitary fish and groups of two or four fish. Four solitary fish, two groups of two fish, and two groups of four fish were observed in each pool.

The first four-fish groups used in the group size experiments were also used in the sequential removal experiments, one group in each pool. In these experiments, I removed the dominant fish at the end of each observation day so that groups of four, three, two, and one fish were observed on consecutive days.

Results

Ranking of Positions

The hypothesis that Arctic grayling rank feeding positions according to desirability was strongly supported by results of both the group size (Fig. 1) and the sequential removal experiments (Fig. 2). The prediction that positions would be added as group size was increased from one to four fish and the prediction that groups of the same size would use the same set of positions were met in almost all cases. Using these results it was possible to determine the rank desirability of the first four feeding positions in Yellow Flower Pool and the first three positions in Bedrock Pool (as shown in Fig. 2). The only possible exceptions to these results were the smallest fish in the four-fish groups observed in Bedrock Pool. Both these fish roamed from one position to another, never settling on one position for long and rarely feeding.

Sorting between Positions

The hypothesis that competition sorts fish between positions until the dominance rank of each fish equals the rank desirability of its position was also strongly supported. Using results

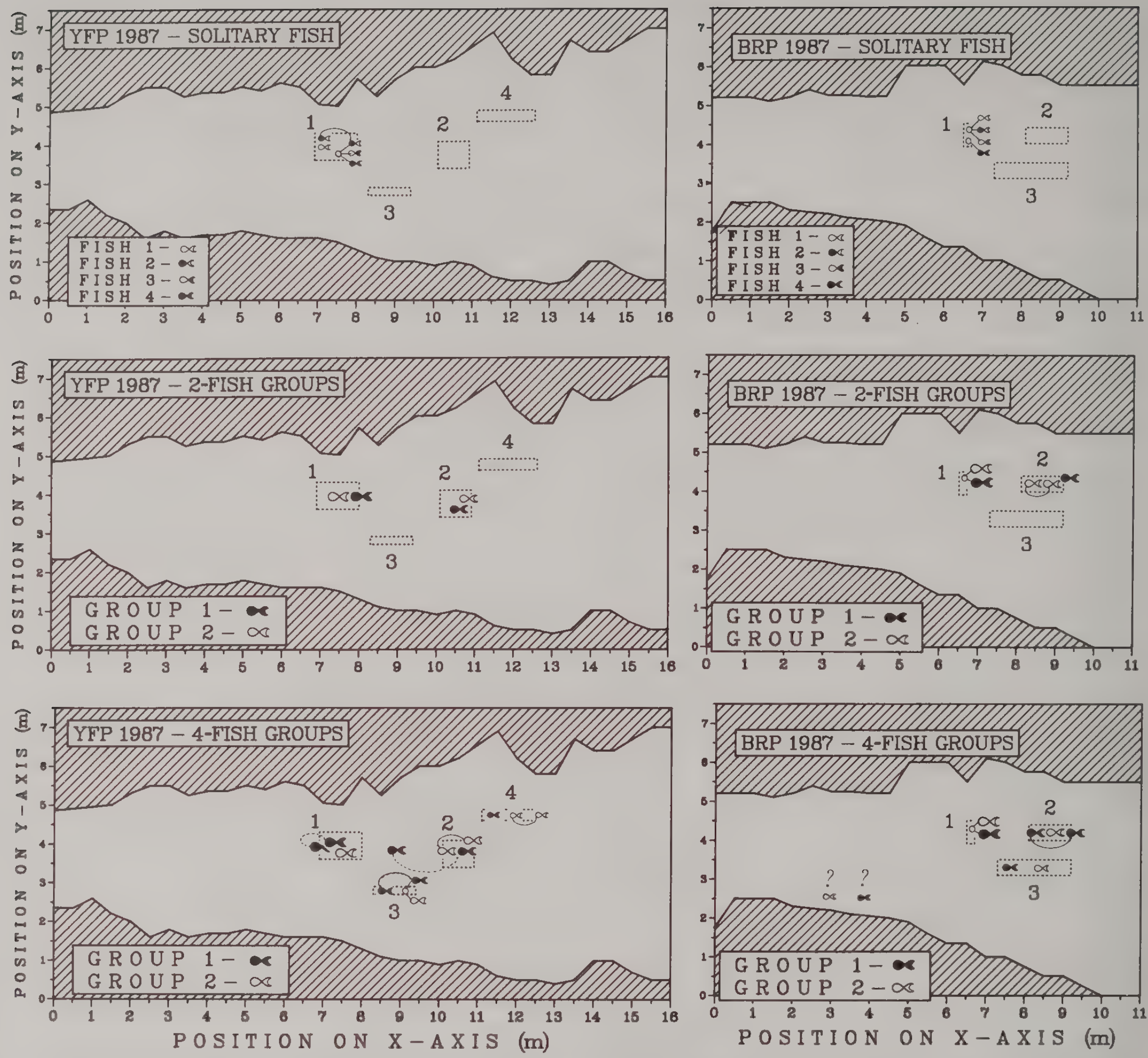

FIG. 1. Results of the group size experiments for Yellow Flower Pool (YFP 1987) and Bedrock Pool (BRP 1987). The locations of the positions chosen by fish are shown by the symbols, and symbol size indicates dominance rank. Curved solid lines connect alternative positions regularly used by the same fish. Curved broken lines connect primary positions with positions that were rarely used. The question marks over the smallest fish in the four-fish groups observed in Bedrock Pool indicate that these fish never settled on a feeding position. The numbered boxes show the location and rank desirability of each position.

from the group size experiments I found a perfect correlation between the dominance rank of a fish and the rank desirability of its position ($P < 0.001$ using Spearman's rho). In the sequential removal experiment the prediction that, following each removal, fish would move into the positions previously occupied by the individual immediately above them in the hierarchy was matched in Bedrock Pool and closely matched in Yellow Flower Pool (Fig. 2).

Discussion

The results of this study demonstrate that Arctic grayling rank feeding positions according to desirability and that competition sorts fish such that the dominance rank of each individual matches the rank desirability of its position.

The behavior of the smallest fish in each of the four-fish groups observed in Bedrock Pool is the only result that does not easily fit into this explanation. Apparently these fish could not settle on a single "fourth-ranked" position and were almost never observed to feed. Perhaps the physical uniformity of the positions available to them meant that there was no real basis for ranking. Alternatively, it is possible that from the fish's point of view, there was no fourth-ranked position in the pool and that these fish were "refugees" unable to find a position in the pool but prevented from leaving by the blocknets.

The experiments in this study support the conclusions that Newman (1956), Vascotto and Morrow (1973), and Fausch (1984) drew from their studies on distribution patterns of drift-feeding stream salmonids. However, these results do not agree with the conclusions of Jenkins (1969) or Bachman (1984). They found little or no evidence for the sorting of fish between

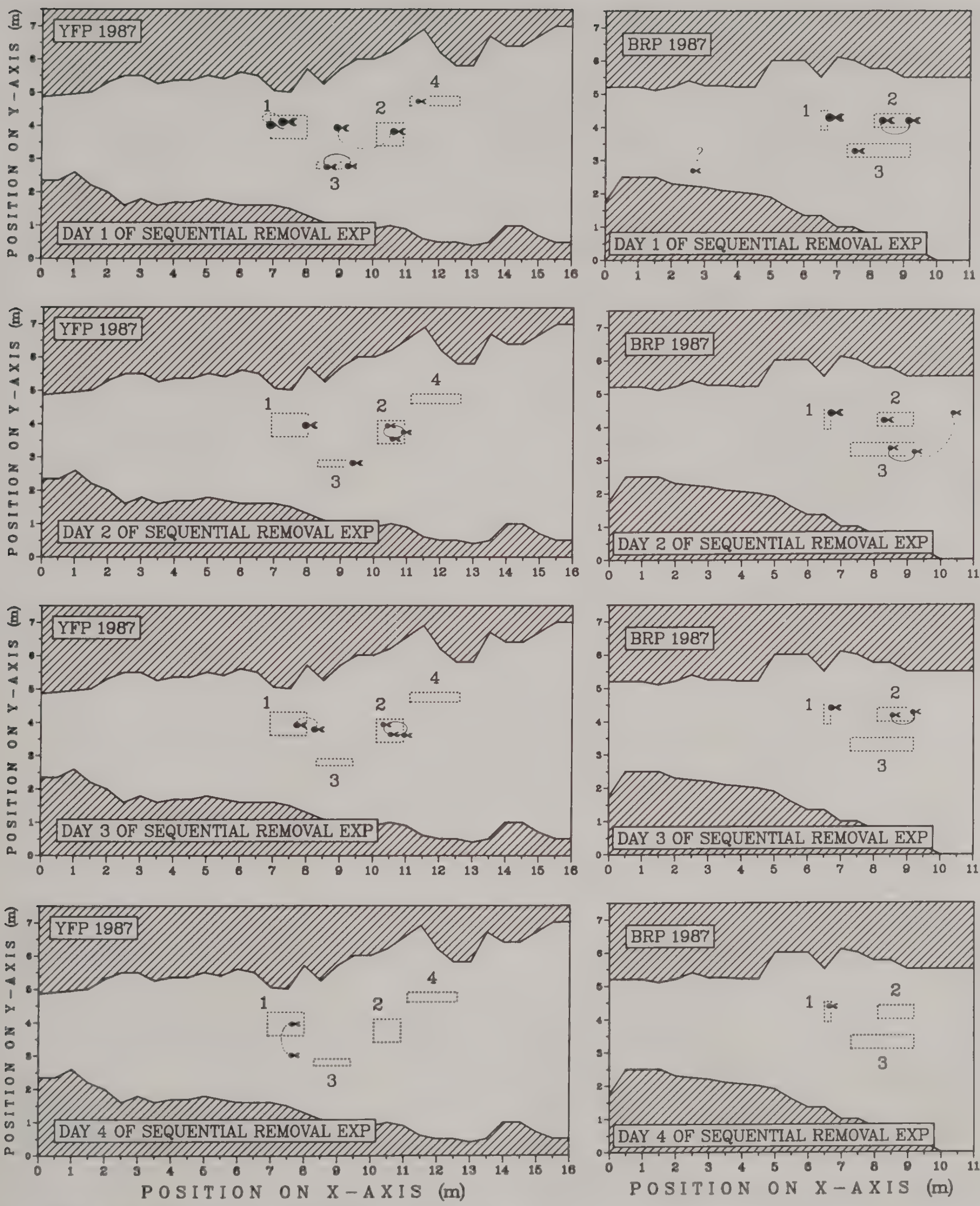

FIG. 2. Results of the sequential removal experiments for Yellow Flower Pool (YFP 1987) and Bedrock Pool (BRP 1987) showing the positions occupied by the original group of four fish and by progressively smaller groups on subsequent days of the experiment. The locations of the positions chosen by fish are shown by the symbols, and symbol size indicates dominance rank. Curved solid lines connect alternative positions regularly used by the same fish. Curved broken lines connect primary positions with positions that were rarely used. The question mark over the smallest fish on the first day of the experiment in Bedrock Pool indicates that this fish never settled on a feeding position. The numbered boxes show the location and rank desirability of each position. Note that day 2 in Yellow Flower Pool is the only time when the dominance rank of each fish did not correspond to the rank desirability of its position; on this day the second fish in the hierarchy occupied the third most desirable position and the third fish in the hierarchy occupied the second most desirable position.

ranked positions, and both contend that this process is unimportant in determining distribution patterns (even though Jenkins found that the dominant fish did occupy a top-ranked position).

How can these conflicting conclusions be explained? One possibility is that the fish in Jenkins' and Bachman's studies did not rank positions because they all provided equal NEI. This is the explanation that the authors themselves favor. Habitat uniformity could account for the lack of ranking in Jenkins' study because most of the positions were in riffles and probably shared similar physical characteristics. However, the habitat map in Bachman's study shows considerable differences in depth (and presumably velocity) between different feeding positions, and so the habitat uniformity argument probably does not explain the apparent absence of ranking. Bachman's study did reveal that individual brown trout were sometimes faithful to the same feeding positions for several years. Perhaps this site fidelity (the function of which is unknown) is of overriding importance in determining the distribution pattern of these fish.

This study shows that the sorting of fish among ranked positions can explain the distribution patterns adopted by hierarchies of drift-feeding stream fishes in some situations. In a companion paper (Hughes 1992) I investigate the processes that determine the location and ranking of these positions.

Acknowledgements

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Selection of Positions by Drift-Feeding Salmonids in Dominance Hierarchies: Model and Test for Arctic Grayling (*Thymallus arcticus*) in Subarctic Mountain Streams, Interior Alaska

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In this work I describe a model to predict position choice by each individual in a dominance hierarchy of drift-feeding stream salmonids. This is an adaptation of Hughes and Dill's model (1990. Can. J. Fish. Aquat. Sci. 47: 2039–2048) of position choice by solitary fish. I have included the effect that prey consumption, lateral diffusion of drifting invertebrates, and entry of invertebrates into the drift have on the density of prey downstream of feeding fish and the restrictions that dominant fish place on freedom of choice by their subordinates. I assume that each fish chooses the most profitable position that its rank in the hierarchy will allow. There was an encouraging match between the distribution patterns predicted by the model and the distribution patterns actually adopted by Arctic grayling (*Thymallus arcticus*) in two pools of a mountain stream. This result suggests that Arctic grayling locate and rank positions based on their profitability. The predictions of reduced models, and the location of positions in relation to bottom topography and current flow, suggest that the physical habitat forms the template for distribution patterns by determining the location and ranking of the most profitable positions.

Dans cette étude, je décris un modèle permettant de prédire le choix de position de chaque individu dans une hiérarchie de dominance parmi des salmonidés de rivière se nourrissant au fil de l'eau. Il s'agit d'une adaptation du modèle de Hughes et Dill (1990. J. can. sci. halieut. aquat. 47 : 2039–2048) du choix de position du poisson solitaire. J'y ai inclus l'effet qu'ont la consommation de proies, la diffusion latérale des invertébrés et l'entrée des invertébrés dans le courant sur la densité des proies en aval du poisson qui se nourrit et les restrictions qu'imposent les poissons dominants à la liberté de choix des subordonnés. Je prends pour acquis que chaque poisson choisit la position la plus profitable que lui permet son rang dans la hiérarchie. J'ai observé une concordance encourageante entre les patrons de distribution prédits par le modèle et ceux qui ont été réellement adoptés par l'ombre arctique (*Thymallus arcticus*) dans deux bassins d'une rivière de montagne. Ce résultat semble indiquer que les ombres déterminent et classent les positions en fonction de l'intérêt qu'elles présentent. Les prédictions des modèles après réduction, et l'emplacement des positions par rapport à la topographie du fond et au débit du courant, semblent indiquer que l'habitat physique constitue le gabarit sur lesquels se modèlent les patrons de distribution puisqu'il fixe l'emplacement et le classement des positions les plus profitables.

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Several studies have shown that drift-feeding salmonids in dominance hierarchies rank feeding positions according to desirability and that competition sorts fish so the dominance rank of each individual matches the rank desirability of its position (Newman 1956; Vascotto and Morrow 1973; Fausch 1984; Hughes 1992). If we understood the processes that determine the location and ranking of these positions we could explain the distribution patterns adopted by these fish. In this study I present a foraging model that shows how physical habitat provides the template for these distribution patterns by determining the location and ranking of the most profitable feeding positions.

Previous work has shown the importance of social behavior in spacing out groups of drift-feeding salmonids (Newman 1956; Kalleberg 1958; Chapman 1962; Jenkins 1969; Slaney and Northcote 1974; Dill et al. 1981; Bachman 1984; Grant and Kramer 1990), but much less is known about the processes that determine the location and ranking of the positions these fish use. To date, Fausch (1984) provides the most complete account. His study suggested that coho salmon (*Oncorhynchus kisutch*) locate and rank positions based on potential net energy intake rate (NEI), thus explaining the adaptive value of position choice. His use of a foraging model also goes some way to explaining how water velocity and prey density determine NEI, although his model cannot be used to predict the location and ranking of positions (see Hughes and Dill (1990) for more discussion of Fausch's model).

In this work I adapt Hughes and Dill's (1990) model, for position choice by solitary fish, to predict the location and ranking of the positions used in hierarchies containing two or more fish. To do this I include the effect that prey consumption, lateral diffusion of drifting invertebrates, and entry of invertebrates into the drift have on prey density downstream of a feeding fish, and the restrictions that dominant fish place on freedom of choice by their subordinates. To test the hypothesis that fish locate and rank positions on the basis of potential NEI, I compare the location and ranking of positions predicted by

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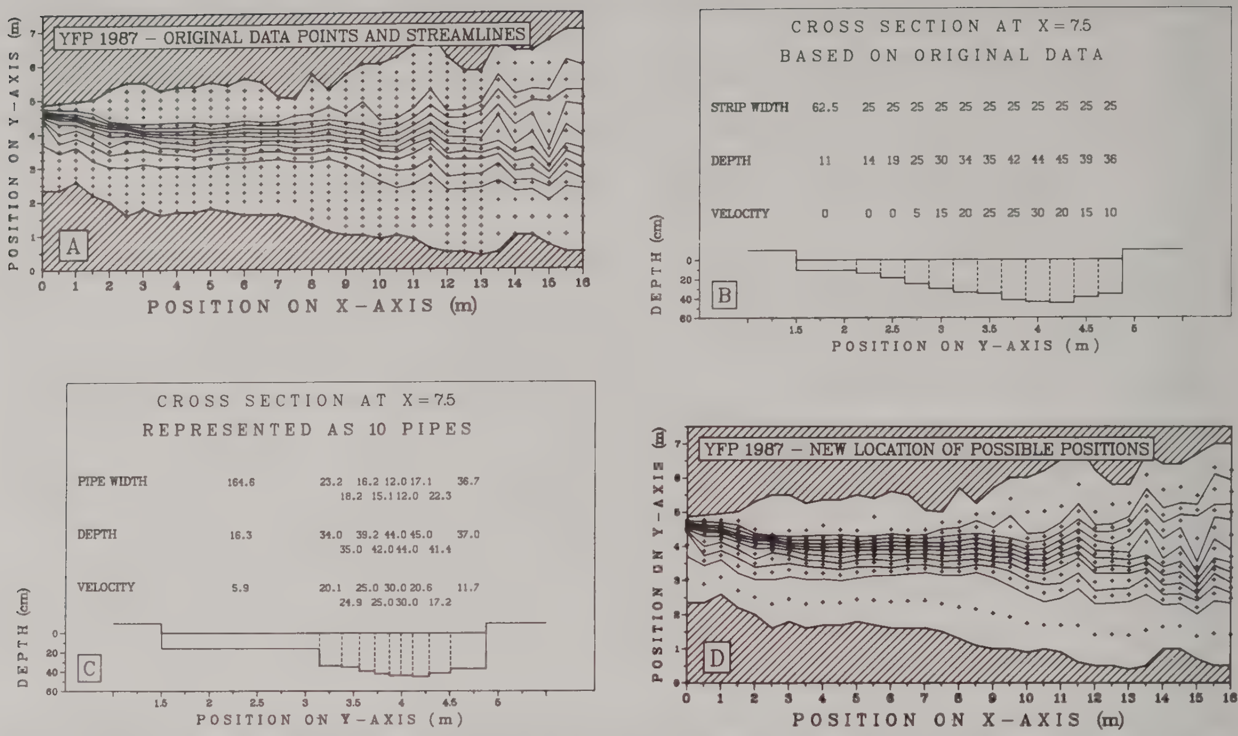

FIG. 1. Example of how the original depth and velocity measurements are transformed to describe the pool as a series of ''pipes'' separated by imaginary vertical walls or ''streamlines.'' (A) Locations at which depth and velocity measurements were taken in one of the study pools (Yellow Flower Pool 1987); flow is from left to right. There are 33 cross sections, and measurements were taken at 0.25- or 0.5-m intervals along each cross section. The nine streamlines drawn through these points divide the pool into 10 pipes, each pipe carrying ⅒ of the stream discharge. To calculate the path of these streamlines, each cross section is initially visualized as a series of strips centered on the location at which water depth and velocity were measured and characterized by these two measurements (as in Hughes and Dill 1990). (B) Sixteenth cross section (*X* coordinate = 7.5 m) represented in this way. The *Y* coordinate at which each of the nine streamlines must intersect the cross section, in order to divide it into 10 pipes with equal discharge, is then calculated. Once these coordinates have been determined for all the cross sections the path of each streamline is known. (C) A new description for each cross section is developed in which pipes replace strips. Each pipe is characterized by water depth and velocity and bounded by the streamlines. The water depth in each pipe at each cross section is calculated as the weighted mean depth of the original strips that contributed to that pipe. The water velocity in each pipe at each cross section is calculated from pipe width, pipe depth, and pipe discharge. (D) The coordinates of possible feeding positions are calculated. These positions are located along each of the 33 cross sections, with one position in the center of each pipe.

the model with the location and ranking of the positions actually selected by Arctic grayling (*Thymallus arcticus*) in the pools of a mountain stream. To examine the effect of the individual processes included in the model, I compare the predictions of the full model with the predictions of the appropriate reduced models. Finally, to determine the way in which the physical habitat acts as the template for fish distribution, I analyze the relationship between bottom topography and current flow and the location of observed and predicted positons.

Methods

Habitat Description

Hughes and Dill (1990) described the habitat using a series of cross sections, each composed of a variable number of vertical strips. While this description is convenient when predicting the position of a single fish it is not so suitable for a model that predicts the distribution of several fish because of the difficulties it creates when modelling processes dependent on the pattern of water flow, such as turbulent mixing of invertebrates downstream of a feeding fish. To make modelling of these processes more tractable I processed the original cross section data to provide a new description of the habitat in which the pool is described as a number of ''pipes'' separated by ''streamlines'' (both terms in the sense of Vogel 1983). The methods involved in this transformation are described in Fig. 1. Although the series of cross sections produced by this transformation are now defined differently than by Hughes and Dill (1990) the methods they developed to calculate capture areas can still be used without modification.

For clarity I use 10 pipes to describe the pool while illustrating how the model works, but I used 25 pipes in the simulations when actually predicting fish distribution. This number provides enough positions to cover the area used by the fish in the study pools while still allowing a reasonable run time on the computer.

Spatial Variation in Drift Density

Hughes and Dill (1990) assumed that invertebrate drift density was the same at all points in a pool. This is probably a fair assumption to make when predicting position choice by a single fish but not when predicting the position choice of additional

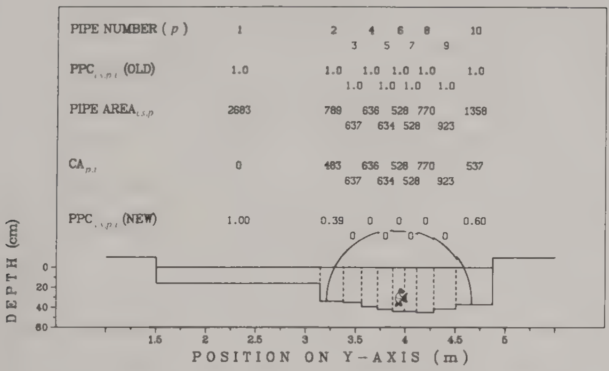

FIG. 2. Calculation of the effect of fish feeding on prey abundance. The fish (26 cm fork length) is holding position in pipe 6 on cross section 16 (X coordinate = 7.5 m). Calculation of its influence on the abundance of prey in size class i = 3 is illustrated. The jagged semicircle shows the maximum capture distance ($MCD_{p,i}$) of the fish to prey in this size class (Hughes and Dill (1990) described how to calculate $MCD_{p,i}$). The capture area for prey in each of the pipes ($CA_{p,i}$) is the overlap of this semicircle with pipe p. Once the $CA_{p,i}$ are known the effect of the fish on the density of prey in each pipe can be calculated as

$$PPC_{cs,p,i}(NEW) = \frac{(PIPEAREA_{cs,p} - CA_{p,i}) \cdot PPC_{cs,p,i}(OLD)}{PIPEAREA_{cs,p}}$$

where $PIPEAREA_{cs,p}$ are the cross sectional areas of the pipes at this cross section, $PPC_{cs,p,i}(OLD)$ is the proportional prey abundance in the pipes at this cross section before the effect of the fish's feeding has been calculated, and $PPC_{cs,p,i}(NEW)$ are the values after the effect of feeding has been calculated. In this example the $PPC_{cs,p,i}(OLD)$ all equal 1 (indicating 100% of unexploited prey density), although the equation works for any values of $PPC_{cs,p,i}(OLD)$.

fish because a feeding fish will influence the density of prey further downstream. To predict position choice by additional fish it is necessary to keep track of this spatial variation in drift density. To do this I assigned a value between 0 and 1, for each prey size class, to each of the possible positions. This number represents the density of prey at that position as a proportion of the unexploited prey abundance or $PPC_{cs,p,i}$. The subscript *cs* represents the number of the cross section containing the position, counting from the head of the pool; p is the number of the pipe containing the position, counting from the left bank looking upstream; and i is the size class of prey (i = 1,. . .,3; after Hughes and Dill 1990). $PPC_{cs,p,i}$ can be converted to the actual prey density by multiplication with the unexploited drift density for prey in size class i or PC_i (Hughes and Dill 1990).

Drift Removal by Feeding Fish

Drift-feeding fish remove invertebrates, which influences the density of drift downstream. The method I used to model this removal is explained in Fig. 2. I assumed that fish are 100% efficient at catching prey that pass through their capture area. This assumption is supported by the work of Wankowski (1981) and Dunbrack and Dill (1984) which demonstrates very high capture rates out to the edge of a fish's capture area, followed by a sharp, steplike decline. However, capture rates could be significantly less than one in some situations. This can easily be accounted for within the framework described in Fig. 2.

Lateral Diffusion of Invertebrates

The variation in prey abundance between neighboring pipes produced by a feeding fish will not persist unchanged for the length of the pool because lateral diffusion will even out the differences. Ciborowski (1983) has shown how the rate of lateral diffusion can be estimated using S_{LD}, the standard deviation of the lateral distance travelled by invertebrates, released from a single point, after travelling a known distance downstream. The way I used this concept to model the effect of lateral diffusion on prey density downstream of a feeding fish is described in Fig. 3; Ciborowski's equation for S_{LD} is given in Table 1.

Entry of Insects into the Drift

Lateral diffusion is not the only process that influences the density of invertebrates downstream of a feeding fish; the entry of invertebrates into the drift will increase drift density when $PPC_{cs,p,i} < 1$, and the net movement of invertebrates into the drift will continue until $PPC_{cs,p,i} = 1$. The dynamics of this process have been expressed mathematically by McLay (1970) and Elliott (1971). Based on their equations I developed a relationship for the change in prey abundance caused by resuspension of drift as the water in a pipe passes from one cross section to the next (Table 1). I used this relationship to model the way that entry of invertebrates into the drift influences prey abundance downstream of a feeding fish (Fig. 4). The combined effect of fish feeding, lateral diffusion, and drift resuspension on the density of a single size class of prey downstream of a feeding fish is shown in Fig. 5.

Social Restrictions on Position Choice

Dominant fish restrict the positions available to their subordinates. This process is very important in determining the distribution pattern of fish in a dominance hierarchy. It means that a fish is not necessarily free to select the position that maximizes its NEI but has to settle for the best position outside of the "restricted area" imposed by dominant fish.

While several studies have determined the size and shape of the areas defended by juvenile stream salmonids in territorial mosaics (Kalleberg 1958; Slaney and Northcote 1974; Dill et al. 1981) there is no comparable work on larger fish in dominance hierarchies. In addition, my observations of Arctic grayling have convinced me that the territorial mosaic concept that has proved so productive with juvenile salmonids cannot explain the way social behavior spaces members in hierarchies made up of adult and subadult fish (see Bachman (1984) for further discussion about the utility of the territory concept for larger fish). This lack of any well worked out relationship has led me to develop a set of rules with which to determine the shape of the restricted area, based on the occasional observations of Arctic grayling social interactions that I have made in the pools of Twelvemile Creek during the experiments described in Hughes and Dill (1990) and Hughes (1992). These rules, and the logic behind them are as follows.

The dominant Arctic grayling in a pool is very intolerant of subordinates that attempt to feed at positions upstream of its own, unless the subordinate is considerably to one side of the pipe occupied by the dominant fish. To model this intolerance I gave the dominant fish in the pool a defended area that extends upstream from its feeding position to the head of the pool and 156 cm to either side of the center of the pipe containing its position. This rule prevents a subordinate fish from selecting any position where prey would pass through its reaction field before they passed through the reaction field of the dominant

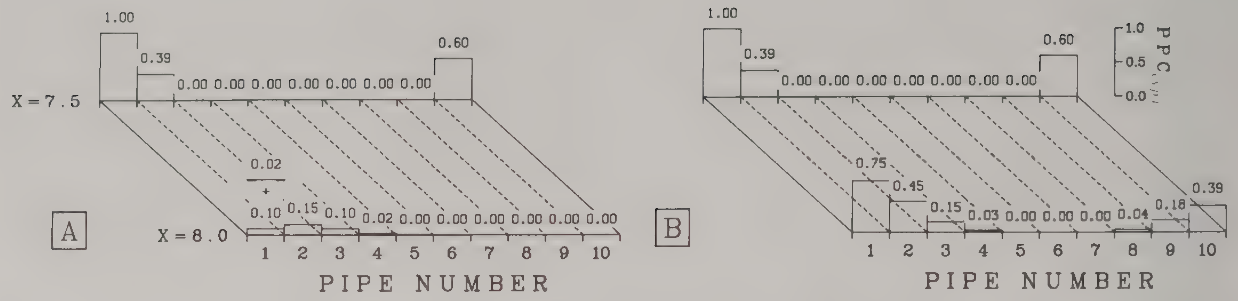

FIG. 3. Calculation of the effect of lateral diffusion on the distribution of drifting insects in size class $i = 3$ as they travel the 0.5 m from one cross section to the next. For the purposes of this calculation the widths of all pipes are assumed to be equal and uniform. Median pipe width was used; this is 23 cm when 10 pipes are used to describe Yellow Flower Pool (1987). The dispersion of invertebrates in each of the donor pipes at cross section 16 (X coordinate $= 7.5$ m) among the recipient pipes at cross section 17 (X coordinate $= 8.0$ m) is calculated using the standard deviation of the lateral distance travelled by invertebrates as they move 0.5 m downstream (S_{LD}) and the standard normal distribution. S_{LD} was calculated using Ciborowski's (1983) equation (Table 1) and was 22 cm in this pool. (A) The $\text{PPC}_{cs,p,i}$ for pipe 2 is redistributed as water flows from cross section 16 to cross section 17. The distance from the center of pipe 2 to its boundaries with neighboring pipes is 11.5 cm, and the standard normal distribution shows that if $S_{LD} = 22$, then 38% of the prey that were in pipe 2 at cross section 16 will remain at this pipe at cross section 17. This means that pipe 2 at cross section 16 will contribute $0.38\ \text{PPC}_{16,2,3} = 0.38 \times 0.39 = 0.15$ to the final value of $\text{PPC}_{17,2,3}$. The same logic, using the distance between the center of the donor pipe and the neighboring pipe boundaries, is used to apportion the entire $\text{PPC}_{16,2,3}$ among the pipes at cross section 17. The contribution of 0.02, "suspended" over pipe 1, shows how the edges of the cross section are treated like a mirror "reflecting" drifting invertebrates back towards the center of the current (as suggested by Smith 1975); the "suspended" 0.02 is added to the value of 0.10 to give the total contribution of $\text{PPC}_{16,2,3}$ to $\text{PPC}_{17,1,3}$. This redistribution of $\text{PPC}_{cs,p,i}$, from donor pipe to recipient pipes, is repeated for all the pipes along the donor cross section. (B) The contributions to each pipe at the recipient cross section are then summed to give the final result. Notice that the $\text{PPC}_{cs,p,i}$ at cross section 16 sum up to the same amount as the $\text{PPC}_{cs,p,i}$ at cross section 17, showing how these calculations redistribute prey but do not increase or decrease the total number of invertebrates in the drift.

TABLE 1. Equations used to estimate the standard deviation of lateral diffusion for drifting invertebrates (S_{LD}) and the increment in drift concentration due to resuspension of invertebrates from the streambed ($\text{IR}_{cs,p,i}$) as water travels 0.5 m from one cross section to the next. The equation for S_{LD} is from Ciborowski (1983), and I developed the equation for $\text{IR}_{cs,p,i}$ from the equations to predict drift density downstream of a driftnet blockage given in McLay (1970) and Elliott (1971). Both equations are parameterized using the values given by Ciborowski (1983) for live *Baetis tricaudatus* (spring). V_{MEDIAN} is the median water velocity in the pool. $\text{PPC}_{cs,p,i}(\text{OLD})$ is the concentration of prey in size class i (as a proportion of unexploited concentration) in pipe p at cross section cs prior to adding the effect of resuspension of drift from the streambed. $V_{cs,p}$ is the water velocity in pipe p at cross section cs.

Parameter	Units	Equation
S_{LD}	cm	$S_{LD} = -0.560 + 0.659 \cdot \sqrt{0.5} + 0.0103 \cdot V_{\text{MEDIAN}}$
$\text{IR}_{cs,p,i}$	None	$\text{IR}_{cs,p,i} = (1 - e^{-R \cdot 0.5}) \cdot (1 - \text{PPC}_{cs,p,i}(\text{OLD}))$ where $R = 8.01 \cdot V_{cs,p}^{-1.07}$

fish (lateral diffusion neglected) because the reaction distance of fish to the largest size class of prey is about 78 cm (Hughes and Dill 1990).

Like the dominant fish in the hierarchy, the No. 2 fish will sometimes swim 4 or 5 m to displace a subordinate that is directly upstream of its own position. However, the No. 2 fish is more tolerant than the dominant fish because it will allow subordinates to occupy positions upstream of its own as long as they are more than 60 cm to one side of the pipe occupied by the No. 2 fish (see fig. 1 and 2 in Hughes companion paper). For these reasons I gave the No. 2 and lower ranking fish a defended area extending upstream from their feeding positions to the head of the pool, but only 60 cm to either side of the center of the pipe containing their feeding position. This technique of assigning restricted areas is illustrated in Fig. 6.

These rules for determining restricted areas are not as objective as the methods used to model spatial variations in drift density, but they do give a reasonable description of Arctic grayling behavior, and at present no independently derived methods are available.

Predicting Arctic Grayling Distribution

The position choice of the dominant fish is predicted first, followed by the choices of successively lower ranking fish. Each fish is assigned to the position that the model predicts will maximize its NEI, with the constraint that no fish can occupy the "restricted area" defended by higher ranking individuals. To find this position, predicted NEI is calculated for all possible positions each time a fish is being placed. NEI is calculated almost exactly as described in Hughes and Dill (1990) except that, in keeping with the modifications and changes in notation described in this paper, their equation (2) for calculation of the fish's gross energy intake rate (GEI) is now more conveniently expressed as

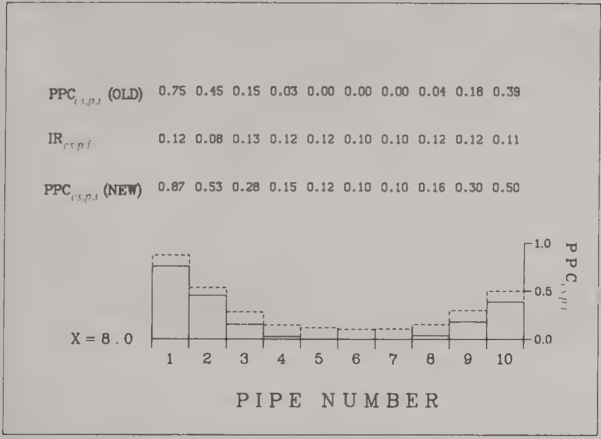

FIG. 4. Modelling the effect of resuspension of invertebrates from the streambed on prey abundance. Cross section 17 (X coordinate = 8.0 m) is shown and these calculations begin where the calculations of Fig. 3 leave off. The effect of drift resuspension on prey abundance at a cross section is determined after the calculations of lateral diffusion and downstream transport from the cross section immediately upstream are complete, but before the effect of lateral diffusion downstream to the next cross section is calculated. I used my adaptation of McLay's (1970) and Elliott's (1971) equations (Table 1) to calculate the increment in $PPC_{cs,p,i}$ due to resuspension ($IR_{cs,p,i}$) as the water travels the 0.5 m from cross section 16 to cross section 17. The $PPC_{cs,p,i}$ ($PPC_{cs,p,i}$(OLD) in this figure) and water velocity in the recipient pipe are used to calculate this increment, rather than values from the donor pipe. This avoids calculation of final values of $PPC_{cs,p,i}$ ($PPC_{cs,p,i}$(NEW) in this figure) larger than 1. The $IR_{cs,p,i}$ is added to $PPC_{cs,p,i}$(OLD) to give $PPC_{cs,p,i}$(NEW). The solid bars show $PPC_{cs,p,i}$(OLD), the increment shown by the broken bars $IR_{cs,p,i}$, and the total height of the bars $PPC_{cs,p,i}$(NEW).

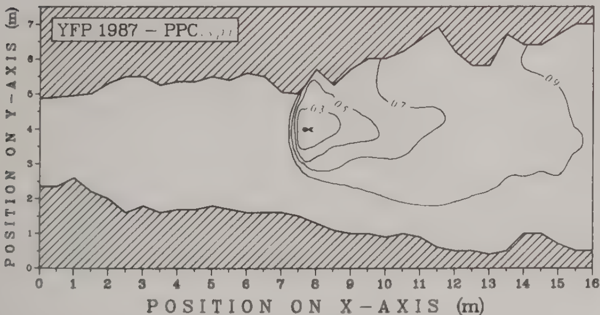

FIG. 5. Effect of fish feeding, lateral diffusion, and resuspension of invertebrates from the streambed on the density of prey in size class i = 3 downstream of a fish (26 cm fork length) feeding in pipe 6 of cross section 16. Prey abundance is expressed as a proportion of the unexploited prey abundance ($PPC_{cs,p,i}$). The spatial variation in abundance of invertebrates will be different for each size class of prey because the reaction distance of the fish depends on prey size (see Hughes and Dill 1990).

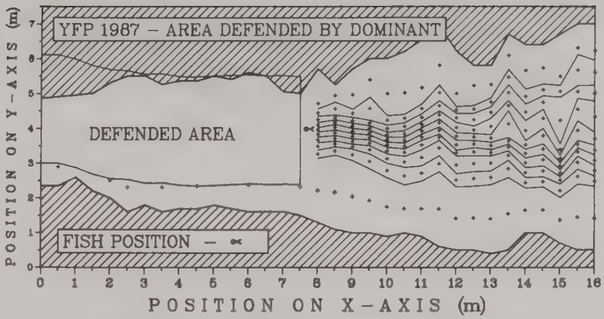

FIG. 6. How the area from which a dominant fish excludes its subordinates is described. The dominant fish has a position in pipe 6 on cross section 16. Its defended area extends upstream of this position to the head of the pool and 156 cm to either side of the center of pipe 6. For lower ranking fish the defended area only extends 60 cm to either side of the pipe containing the fish's feeding position.

$$(1)\quad GEI = \sum_{p=1}^{NPIPES} \sum_{i=1}^{3} CA_{p,i} \cdot V_{cs,p} \cdot PPC_{cs,p,i} \cdot PC_i \cdot PE_i \cdot 3600/1\,000\,000$$

where NPIPES is the number of pipes used to describe the pool, $CA_{p,i}$ is the capture area of the fish for prey in size class i in pipe p, $V_{cs,p}$ is the water velocity at pipe p in cross section cs, $PPC_{cs,p,i}$ is the density of prey in length class i at pipe p in cross section cs as a proportion of its unexploited concentration, PC_i is the unexploited prey concentration of prey in size class i, PE_i is the energy content of each prey in length class i, and the 3600/1 000 000 term is necessary because $CA_{p,i}$ and $V_{cs,p}$ have units of centimetres and seconds, while PC_i and GEI have units of metres and hours. NEI is then calculated as GEI − SC where SC is the fish's swimming cost. The necessary definitions, equations, and parameter values for Arctic grayling are given in Hughes and Dill (1990).

After a fish has been assigned to a position, values of $PPC_{cs,p,i}$ are recalculated for all the positions in the pool and the area that the fish defends is defined, before predicting the position of the next fish. I recalculate $PPC_{cs,p,i}$ by starting at the top of the pool and working downstream, one cross section at a time. When a cross section contains a fish's position the effect of this fish on the density of drift in that cross section is calculated (as described in Fig. 2). Next the combined effects of lateral diffusion and resuspension on $PPC_{cs,p,i}$ are calculated down to and including the next cross section to hold a fish (as described in Fig. 3 and 4). The effect of this fish on $PPC_{cs,p,i}$ is then calculated and the process is continued to the end of the pool. If there are two or more fish on a single cross section the effect of each of them on $PPC_{cs,p,i}$ is calculated in turn, starting with the highest ranking fish, before continuing downstream.

Testing the model

I tested the model by comparing the distribution patterns it predicted in two pools of Twelvemile Creek (Bedrock Pool 1987 and Yellow Flower Pool 1987) with the distribution patterns actually adopted by Arctic grayling in these pools. Hughes and Dill (1990) described Twelvemile Creek and the methods used to map the pool habitat. Values for median pipe width were 8.5 cm in Yellow Flower Pool and 7.5 cm in Bedrock Pool (25 pipes used to describe flow), median water velocity was 30 cm·s^{-1} in Yellow Flower Pool and 45 cm·s^{-1} in Bedrock Pool, and the standard deviation of lateral diffusion was estimated as 0.22 m in Yellow Flower Pool and 0.37 m in Bedrock Pool. The methods used to determine the distribution patterns actually adopted by Arctic grayling in these pools are described in Hughes (1992). Predictions were made for a group of four fish in Yellow Flower Pool and three fish in Bedrock Pool. The fork lengths of these fish were, in order of dominance rank, 26, 22.5, 24, and 20.5 cm in Yellow Flower Pool and 28.5, 24, and 22.5 cm in Bedrock Pool. These lengths and ranks

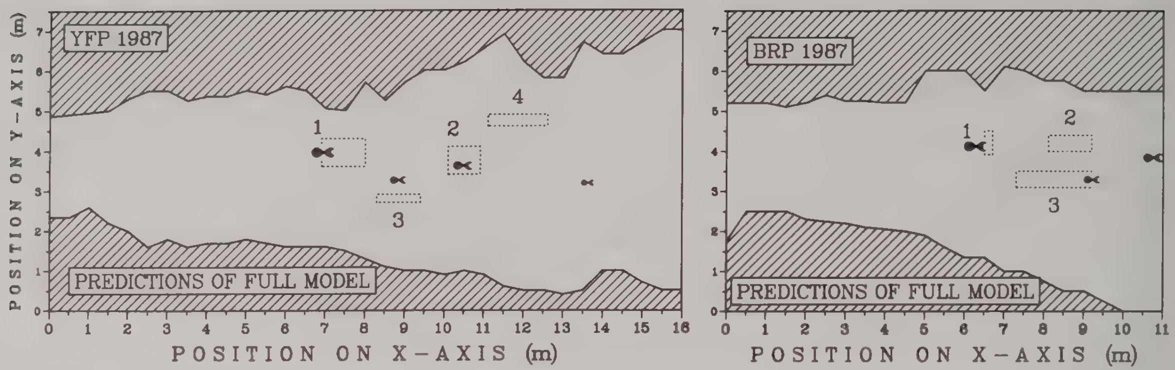

FIG. 7. Comparison of the distribution pattern predicted by the model and the distribution pattern actually adopted by the fish in Yellow Flower Pool (YFP 1987) and Bedrock Pool (BRP 1987). The predicted positions are indicated by the fish symbols, where symbol size represents dominance rank. The numbered boxes show the location and rank desirability of positions actually used by the fish (see Hughes 1992). For a perfect match between the predicted and observed results the largest fish symbol should lie within box 1, the second largest fish symbol in box 2, and so on.

correspond to the first four-fish group observed by Hughes (1992) in Yellow Flower Pool and the largest three fish in the first four-fish group he observed in Bedrock Pool.

To examine the influence individual processes have on the distribution pattern predicted by the model I evaluated versions without the effects of prey capture, lateral diffusion, resuspension of drift, and restricted areas. Although some of these versions are unrealistic the results of this exercise are helpful in explaining the distribution pattern of fish in a dominance hierarchy.

To determine the extent to which the bottom topography of the pool and the pattern of water flow provide the template for fish distribution I examined the distribution of the observed and predicted positions in relation to these habitat features.

Results

Observed versus Predicted Distribution Patterns

The match between predicted and observed patterns of fish distribution is evaluated in Fig. 7 and 8. In both pools the predicted distribution matches the observed distribution quite well.

In Yellow Flower Pool the model accurately predicts the location and ranking of the two most desirable positions in the pool and makes fairly accurate predictions for the third position (predicted positions are a little too close to the center of the current) but is wide of the mark for the fourth position (predicted position is too far downstream and too near the center of the current). In Bedrock Pool, predictions for the first and third position were accurate and the predictions for the second ranking position were quite accurate when assessed by the method used in Fig. 8 (6 out of 11 of the predicted positions lie within the target area) but more than 1 m too far downstream when assessed by the method used in Fig. 7.

Predictions of Reduced Models

The distribution patterns predicted by the four reduced versions of the model are shown in Fig. 9. None of the reduced models made more realistic predictions than the full model and in most cases their predictions were much worse. When compared with the full model each of the reduced versions produced characteristic changes in the predicted distribution pattern. The "no prey depletion" model predicted that each fish would choose a position right on the tail of the fish immediately above it in the dominance hierarchy. Predictions of the "no lateral diffusion" model were most similar to those of the full model, the main difference being that the No. 2 fish moved laterally so that they were no longer directly downstream of the No. 1 fish. In Yellow Flower Pool the No. 3 and No. 4 fish also moved to positions further from the center of the current. The "no resuspension" model predicted that subordinate fish would move to positions further upstream and fan out across the pool. The "no restricted area" model predicted that each fish would choose a position directly upstream of the fish immediately above it in the dominance hierarchy.

Distribution Patterns and the Physical Habitat

The location and ranking of both the observed positions and the positions predicted by the full model bear a definite relationship to the bottom topography and current flow in the pool (Fig. 10). In both pools the top-ranked position lies just downstream of the deepest part of the pool in the center of the current. The second-ranked position lies directly downstream of the first, also in the center of the current, and in a small depression in the bottom that "buds" off from the main depression. The third-ranked position is downstream of the first position, level with or upstream of the second position, and to one side of the main flow. The depth contours show that this position is in a "scallop" in the streambed on the more gently sloping side of the pool, so that the fish is occupying the deepest water possible given its distance from the center of the current. The streamlines suggests that there is a distinct lateral component to the flow at these positions. The fourth highest ranking position in Yellow Flower Pool was downstream of all other positions, on the opposite side of the pool from the third position, and in slightly shallower water. Otherwise its physical characteristics were similar to the third-ranked position; it too was in a scallop in the streambed at a position where there was significant lateral flow. Examination of Bedrock Pool suggests that if there were a fourth position it might be at about $X = 10.5$, $Y = 5.0$, which is similar in nature to the fourth position in Yellow Flower Pool. It is intriguing that the third-ranked fish in Bedrock Pool did occasionally use a position in this area as an alternative to its usual position (Hughes 1992: day 2 of sequential removal experiment in Bedrock Pool).

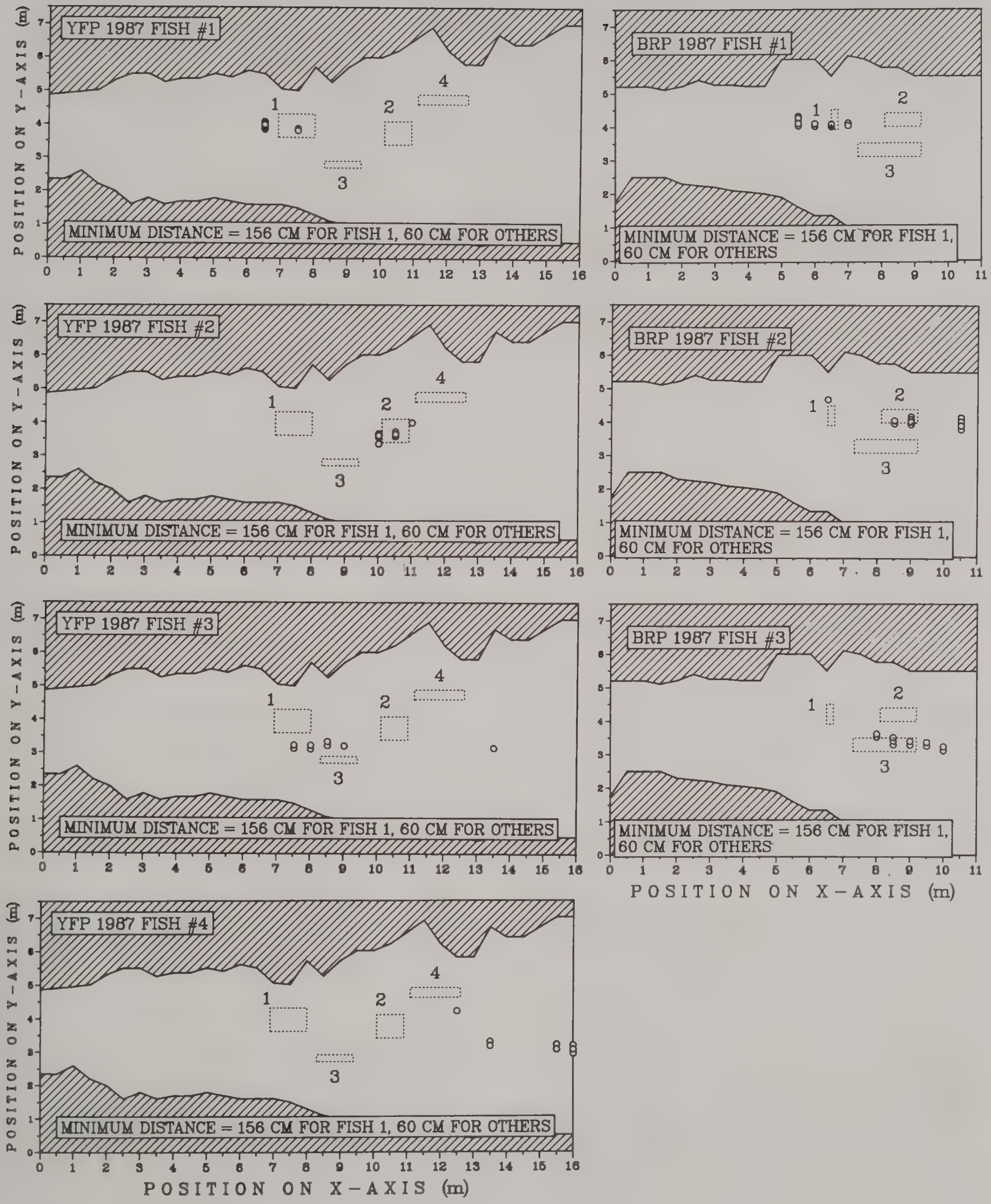

FIG. 8. Comparison between the location of the positions that the model ranked in the top 1% (YFP 1987) or 2% (BRP 1987) of all possible positions with the positions actually used by fish. The circles show the location of the predicted positions, while the numbered boxes show the location and ranking of positions actually used by the fish (see Hughes 1992). The results for each fish in the hierarchy are plotted separately. In a perfect match between predictions and observations the predicted positions for fish No. 1 should cluster within and around box 1, the predicted positions for fish No. 2 should cluster around box 2, and so on.

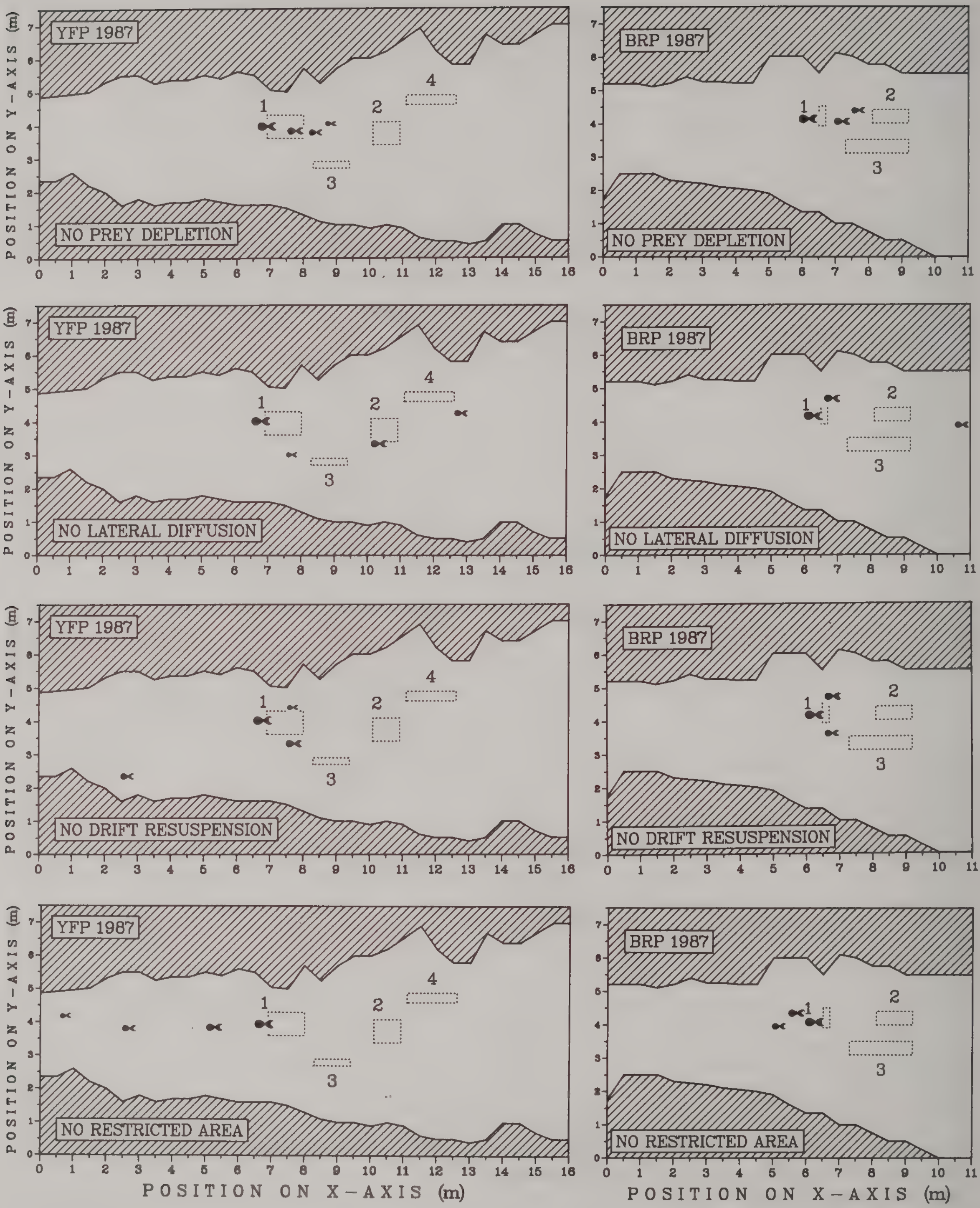

FIG. 9. Distribution patterns predicted by the four reduced models in Yellow Flower Pool (YFP 1987) and Bedrock Pool (1987). The fish symbols show the predicted positions and the size of the symbol corresponds to dominance rank. The numbered boxes show the location and ranking of positions actually used by Arctic grayling in these pools (see Hughes 1992).

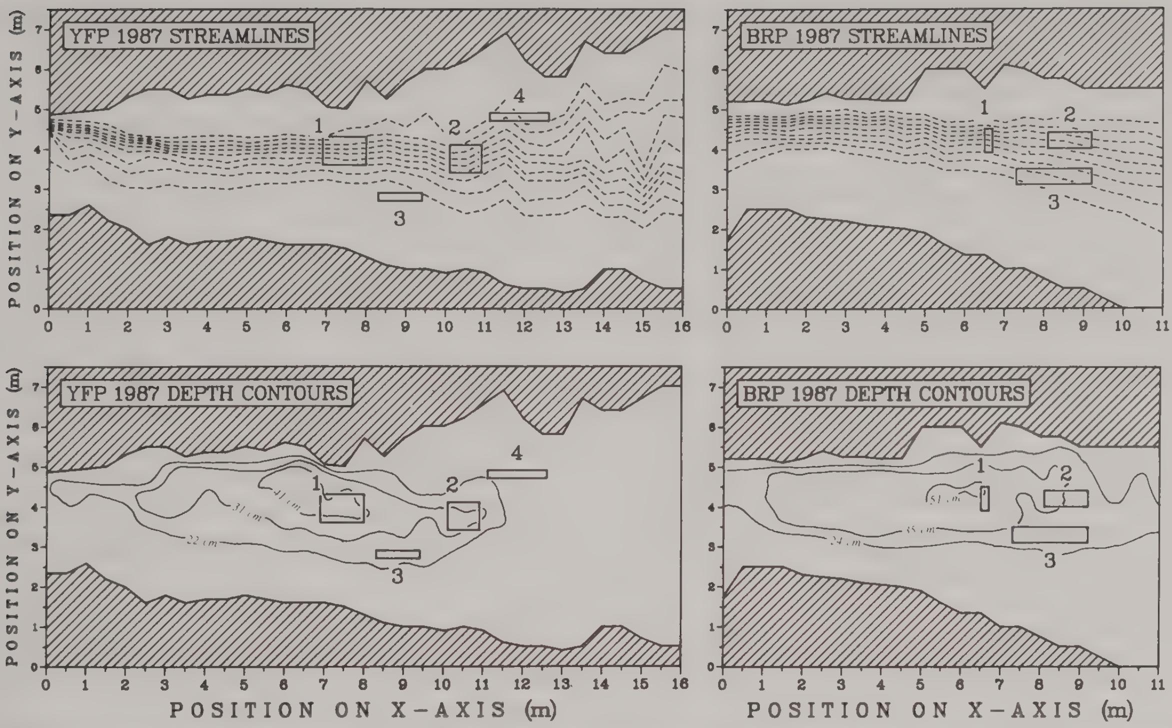

FIG. 10. Depth contours and streamlines for Yellow Flower Pool and Bedrock Pool. The numbered boxes show the location and ranking of positions actually used by Arctic grayling in these pools. The depth contour levels were selected to pick out important features in the bottom topography.

Discussion

This study supports the hypothesis that Arctic grayling select and rank positions based on potential NEI. This conclusion is based on the close fit between the predicted and observed location and ranking of positions (Fig. 7 and 8). These results support Fausch's (1984) conclusions on the adaptive significance of position choice, but they do not support Jenkins' (1969) and Bachman's (1984) view that there are no variations in feeding opportunity between positions. My results also suggest that trade-offs involving predation risk are not important in determining the location of feeding positions, as suggested by Newman (1956), Jenkins (1969), and Fausch and White (1981), since it was not necessary to include the effects of predation risk to make fairly accurate predictions of position choice (see Hughes and Dill (1990) for more discussion).

All four reduced versions of the model made worse predictions than the full model, suggesting that each of the processes included in the model makes a significant contribution to its accuracy. The predictions of the ''no restricted area'' model show that, given freedom of choice, subordinates would select positions directly upstream of higher ranking fish. This demonstrates the importance of social behavior in creating distribution patterns where subordinates occupy positions downstream and/or to the sides of positions occupied by higher ranking fish.

The predictions of the ''no prey depletion'' model show that the reduction in drift density by a feeding fish makes it unprofitable for subordinates to occupy positions immediately downstream. The effect of this process complements the effect of social restrictions on position choice because it spaces fish out downstream and/or laterally behind the dominant fish.

Predictions of the ''no resuspension'' model show that the replenishment of drift density by resuspension induces fish to select positions some distance downstream, but directly in line with, the positions occupied by higher ranking fish. This complements one of the effects of social behavior (spacing fish out downstream) but counteracts another (inducing fish to select positions directly downstream of higher ranking individuals).

Predictions of the ''no lateral diffusion'' model suggest that the redistribution of prey downstream of a feeding fish has a similar effect to resuspension, causing fish to select positions some distance downstream of, but in line with, the positions used by dominants.

The bottom topography of the pool and the pattern of current flow determine the volume of water from which the fish can catch prey and the fish's swimming costs (Hughes and Dill 1990). They also influence the lateral diffusion and resuspension of invertebrates, processes that determine spatial variation in the density of prey. Because of these influences on the factors that determine NEI, these physical characteristics of the pool can be thought of as the template that determines the location and ranking of positions selected by the fish. The importance of the habitat as a template is well illustrated by the relationship between physical characteristics and the location and ranking of positions shown in Fig. 10. Bedrock Pool and the upper 11 m of Yellow Flower Pool are very similar in physical layout and this similarity has produced a corresponding similarity in the location and ranking of predicted and observed positions.

To visualize the way in which the habitat acts as a template for distribution it is helpful to think about the factors influencing the fish's energy intake at a position in the following way. The number of prey a fish sees increases with water depth, water velocity, and the density of prey in the water. The proportion of these prey that the fish is able to capture declines with increasing water velocity, while its swimming costs increase with water velocity (Hughes and Dill 1990). The fish must select a position where the combination of these factors maximizes its NEI and yet complies with the restrictions on its freedom of choice imposed by higher ranking fish.

For the dominant fish this position is just downstream of the deepest point, in the center of the current (see Hughes and Dill (1990) for further discussion). For the second fish the small depression about 2 m directly downstream of the dominant fish apparently provides the best compromise between favorable physical characteristics and prey density. These positions are close enough to the center of the current and the deepest part of the pool to provide desirable water depth and velocity characteristics and yet far enough downstream of the dominant fish's feeding area for resuspension and lateral diffusion to have substantially replenished the density of drifting invertebrates. For the third and fourth fish the best compromise is apparently to hold position in scallops in the streambed at the sides of the pool. Given their distance from the center of the current these positions provide reasonable depth (because they lie in scallops) and flow (because of the lateral water movement at these positions) and receive water that has skirted either side of higher ranking fish's feeding areas; this means that the prey density at these positions is higher than at physically comparable positions immediately downstream of the second fish.

Acknowledgements

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Food of the Alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the Establishment of *Bythotrephes cederstroemi*

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Diets and length–weight relationships of Lake Ontario alewife (*Alosa pseudoharengus*) in 1972 differed from those in 1988; the large cladoceran *Bythotrephes cederstroemi* colonized the lake during the mid-1980's. Microcrustacean zooplankton were the dominant prey of alewife during April–October in 1972 and 1988. Although *Bythotrephes* was not found in 1988 net samples, it replaced other zooplankters in the alewife's diet. Typically, tailspines were the only part of *Bythotrephes* in alewife stomachs; their frequency was high in April–May, diminished rapidly in summer, and was very low by fall. In spring 1988, alewife ≥165 mm were in better condition than in spring 1972, and this may have been due to larger fish feeding more heavily on *Bythotrephes*. Variation in diet among widely separated sampling sites was due to differences in alewife abundance, stability of thermal structure, progress of zooplankton community development, and distance to the mouth of the Niagara River (through which *Bythotrephes* probably enter the lake in summer and fall). In the Great Lakes, inter- and intralake differences in diet clearly exist, and these must be incorporated into models of alewife planktivory to gain an accurate understanding of energy flow between trophic levels.

Étant donné que le régime alimentaire et les relations longueur–poids du gaspareau (*Alosa pseudoharengus*) du lac Ontario ont changé entre 1972 et 1988, on a tenté de déterminer si la colonisation du lac par le gros cladocère *Bythotrephes cederstroemi* vers le milieu des années 1980 était un facteur responsable. D'avril à octobre en 1972 et 1988, les microcrustacés zooplanctoniques étaient la principale proie du gaspareau. Bien que *Bythotrephes* n'était pas présent dans les échantillons recueillis au filet en 1988, il a remplacé d'autres espèces de zooplancton dans le régime alimentaire du gaspareau. Généralement, seules les épines de la queue de *Bythotrephes* étaient retrouvées dans l'estomac des poissons; leur fréquence était élevée en avril et mai, chutait au cours de l'été et était très faible en automne. Au printemps de 1988, les gaspareaux de 165 mm ou plus de longueur étaient en meilleure condition qu'au printemps de 1972; ceci peut être dû au fait que les gros poissons consommaient de plus grandes quantités de *Bythotrephes*. La variation du régime alimentaire entre les sites d'échantillonnage très éloignés l'un de l'autre était le résultat de différences entre l'abondance du gaspareau, la stabilité de la structure thermique, le niveau d'évolution de la communauté zooplanctonique et la distance de l'embouchure de la rivière Niagara (par où *Bythotrephes* entre probablement dans le lac en été et en automne). Il existe manifestement dans les Grands Lacs des différences intralacustres et interlacustres du régime alimentaire, différences qui doivent être incluses dans les modèles de la planctivorie du gaspareau si l'on veut comprendre le transfert d'energie entre les niveaux trophiques.

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Lake Ontario was the first of the Laurentian Great Lakes invaded by the alewife (*Alosa pseudoharengus*). Alewife apparently entered Lake Ontario in the 1860's and have been the dominant fish species there since the 1870's (Smith 1970; Christie and Thomas 1981). They are now an important food of introduced salmonines in Lakes Ontario (Brandt 1986; Elrod and O'Gorman 1991), Huron (Diana 1990), and Michigan (Eck and Brown 1985), and they are the basis of fisheries of considerable economic importance (Talhelm 1987).

In lacustrine systems, alewife are planktivores that readily supplement their diet of zooplankton with other foods such as fish eggs and larvae, insects, and amphipods (Odell 1934; Hutchinson 1971; Kohler and Ney 1980; Wells 1980). In Lake Michigan, Hewett and Stewart (1989) considered about 65% of the diet (wet weight) of adult alewife to be zooplankton during April–October and the rest to be mostly *Mysis* and amphipods. In Lake Ontario, alewife food habits are well documented only for the Bay of Quinte (Hurley 1986); in the main lake, information on alewife food habits is scant (Pritchard 1929), although the fish's diet should be similar to that in Lake Michigan because the invertebrate fauna of the two lakes is similar. The colonization of the Great Lakes by the cladoceran *Bythotrephes cederstroemi* in the 1980's (Bur et al. 1986; Lange and Cap 1986; Sprules et al. 1990; Johannsson et al. 1991), however, has undoubtedly influenced the diet of the alewife. Because this exotic cladoceran is larger than endemic zooplankters, it is highly visible to predators, and because alewife are size-selective planktivores (Wells 1970; Warshaw 1972), *Bythotrephes cederstroemi* should be an important food for them. In central Lake Erie, consumption of zooplankton by yellow perch (*Perca flavescens*) nearly doubled after *Bythotrephes* became abundant (Bur and Klarer 1991). If the diet of alewife in the Great Lakes shifts similarly, predation on benthic macroinvertebrates would decline whereas predation on zooplankton would increase. This might influence productivity of alewife populations because a switch to more pelagic feeding would change the fish's daily temperature regime and thus food consumption and conversion efficiency (Stewart and Binkowski 1986). Such a shift in distribution might also alter the availability of alewife to predators.

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The objective of this study was to determine if food habits and body condition of alewife changed with the colonization of Lake Ontario by *Bythotrephes cederstroemi*. We did this by comparing the diet and length–weight relationship of alewife in 1988 with that in 1972, prior to the establishment of *Bythotrephes* in Lake Ontario. Length–weight relationships can be influenced by fish abundance, so we also compared the magnitude and size structure of alewife populations in the two years. Because any effect of *Bythotrephes* on diet probably varies with season and lake region, we sampled alewife food habits over a broad range of depths at three widely spaced locations from spring through fall to compare spatial and seasonal patterns of alewife planktivory. To determine whether seasonal diet shifts were related to the occurrence of *Bythotrephes*, we attempted to track its abundance by periodically sampling zooplankton in south-central Lake Ontario.

Methods

Collecting Alewife for Food Habits

From May to October 1972, 490 alewife were collected for diet analysis by bottom trawling from the R/V *Kaho*. The fish were subsamples of catches at 33 stations, total depth 9–146 m, along three transects off Hamilton, Ontario, and Rochester and Oswego, New York (Fig. 1). In 1988, 761 alewife were collected for analysis by bottom trawling from the R/V *Kaho* along transects off Olcott, Rochester, and Oswego, New York. Catches were subsampled at 29 stations, total depth 15–110 m, from April to October. In 1972, only adult alewife (≥108 mm) were collected whereas in 1988, adult and subadult alewife (≤107 mm) were collected. The whole fish was preserved in 10% formalin after either injecting 10% formalin into the coelomic cavity (1972) or puncturing the coelomic cavity (1988).

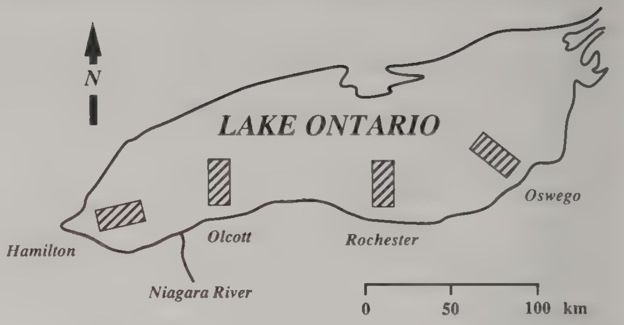

FIG. 1. Locations of sites where alewife were collected from Lake Ontario in 1972 and 1988. The Olcott site was not sampled in 1972, and the Hamilton site was omitted in 1988.

Assessing Alewife Abundance, Size, and Condition

Bottom-trawl nets towed by the R/V *Kaho* to collect alewife in 1972 and in 1988 were similar in dimensions and mesh sizes. Trawl doors differed between years, but the towing vessel and all trawling procedures (e.g. towing speed, warp to depth ratio) were virtually identical. Handling of the catch was also similar; adults and subadults were sorted on the basis of length and then counted separately. Therefore, we assumed that if the alewife catch rate in 1972 differed from that in 1988 ($P < 0.05$), it was due solely to a change in abundance. Catches were transformed by $\log_{10}$ (catch + 1) to help stabilize the variance and to normalize the data before comparing mean catches by using the general linear model program of SAS Institute (1988) to perform an analysis of variance (ANOVA). For this analysis, we used data from April–May only when alewife are closest to bottom (Elrod and O'Gorman 1991) and from only those depths and lake areas (Olcott, Rochester, and Oswego) that were fished in both years. Trawl tows that fit these criteria totaled 12 in 1972 and 23 in 1988.

In each sampling period in 1988, from 13 to 27 bottom-trawl tows were made in each of the three lake ares from which alewife were collected for diet analysis. The depth range fished varied among seasons but was always similar in the three areas in each season. To determine if adult alewife abundance differed between areas, the catches were $\log_{10}$ transformed and the mean catches in each season were compared with ANOVA performed with a general linear model, followed by the Tukey–Kramer multiple comparison test (SAS Institute 1988). We could not determine if alewife abundance along the south shore of Lake Ontario differed among sampling periods because the availability of alewife to the bottom trawl changed with season (Elrod and O'Gorman 1991).

We measured (total length, nearest millimetre) a random sample of adult and subadult alewife from most trawl hauls in April–May in 1972 and 1988. Length samples from those depths and lake areas fished in both years were used to construct length–frequency distributions of adults (n = 1352 in 1972 and 860 in 1988) and subadults (n = 32 and 628). The distributions were compared by use of a Kolmogorov–Smirnov test (SAS Institute 1988).

A small sample of adult alewife from most trawl hauls was measured and weighed (nearest gram) at Olcott, Rochester, and Oswego in April–May and October in 1972 and 1988. Depth ranges fished in spring were 18–110 m in 1972 and 8–150 m in 1988, and depths fished in fall were 9–146 m and 8–150 m. We measured and weighed adults 125–200 mm in spring

($n = 230$ in 1972 and 321 in 1988) but only fish 150–179 mm in fall ($n = 174$ and 303). Fish were placed on ice soon after capture and weighed and measured within 30 h of capture. Lengths and weights were transformed by $\log_{10}$ before calculating length–weight relationships. We used the homogeneity-of-slopes model of the general linear model program of SAS Institute (1988) to perform an analysis of covariance (ANCOVA) for each season. When the F value indicated that the slopes were not significantly different ($P > 0.05$), we used the ANCOVA model of the general linear model program (SAS Institute 1988) to determine if the intercepts differed.

Sampling Zooplankton

Zooplankton collections were made 2 and 20 km from shore at Smoky Point (20 km east of Rochester) and Oak Orchard (51 km west of Rochester) (Fig. 1). Collections were made in April, June, July, September, and October in 1987 and 1988 to document when *Bythotrephes cederstroemi* was abundant. Bottom depths were 22 and 206 m off Oak Orchard and 25 and 196 m off Smoky Point. Zooplankton abundance and composition were determined from vertical hauls with a 0.5-m-diameter, 153-μm-mesh nylon net. Before each plankton haul, we determined temperatures in the water column with a mechanical bathythermograph. At the 2-km sites, the net was lowered to the lake bottom except when thermal stratification was strong, in which case the net was lowered to the top of the thermocline. For sites 20 km offshore, sampling was to a depth of 50 m or to the top of the thermocline if one was formed. Zooplankton were preserved in a sugar–formalin solution (Haney and Hall 1973).

Individual zooplankters were identified to species in all samples (Edmondson 1963; Balcer et al. 1984) and enumerated in one to three 1-mL subsamples. Immature zooplankters (neonates and copepodites) were also counted and measured in all subsamples. Because of their low density and high visibility, all *Bythotrephes* in each sample were counted.

Examining Alewife Stomach Contents

1972

Alewife total length (TL) was measured to the nearest millimetre, and contents of alewife stomachs were identified and counted at 15–30 ×. For some fish, all organisms in the stomach were counted, but for most fish, a subsample was counted. Water was added to the entire contents of an individual stomach to bring the total volume to 20–40 mL. After thorough mixing, a Hensen–Stemple pipette was used to withdraw 1-mL aliquots. The volume of the subsample examined was typically 2.5–20% of the total sample, and total numbers of organisms in the stomach were estimated from the subsample by direct proportion.

1988

Alewife were measured to the nearest millimetre (TL) as in 1972, but we followed a different procedure to estimate total stomach contents. Stomachs were removed and dissected into anterior and posterior segments. We counted only the contents of the anterior (dorsal) limb of the stomach because the contents of the posterior (ventral) limb were digested. Contents of the anterior stomach section were sorted; all microinvertebrates were removed, counted, and, when possible, measured at 20 ×. The remaining microinvertebrate fraction was subsampled as in 1972. At least two to three 1-mL aliquots were withdrawn from a known-volume dilution of the microinvertebrates. We identified (Balcer et al. 1984), counted, and measured all zooplankton in these subsamples by use of an electronic caliper interfaced with a microcomputer (Mills and Confer 1986). Zooplankters were measured from the anterior margin of the helmet to either the base of the tailspine (cladocerans) or the base of the caudal setae (copepods). For macro- and microinvertebrates that were not intact, we found the number of organisms by counting characteristic body parts. For example, the only recognizable body part of *Bythotrephes* in alewife stomachs was the tailspine. *Bythotrephes* has a characteristic kink in its tailspine, and the number of *Bythotrephes* in alewife stomachs was based on counts of spines with the tailspine kink. The approach was similar for *Mysis relicta*; the number eaten was based on counts of characteristic paired eyes.

Contents of the anterior and posterior portions of each alewife stomach were dried separately at 60°C for 48 h and weighed to the nearest 0.01 mg on a Cahn electrobalance. We used the ratio of the dry weight to the number of organisms in the anterior limb to convert dry weight of the posterior limb to number of organisms. Numbers of organisms in the anterior and posterior limbs were combined to determine the total number of prey in an alewife stomach.

Analysis of Diet Data

We applied known length – dry weight regressions (Cornell University Biological Field Station, unpubl. data; Johannsson and O'Gorman 1991) to prey lengths to estimate the dry mass of prey items. When organisms were unmeasurable owing to breakage or digestion, we used average values for the same prey item from alewife examined in the same month at the same site. In 1972, prey organisms were not measured; we calculated the average biomass of individual prey for the various prey organisms at each transect in each month of 1988, and we applied these values to the 1972 organism counts to estimate prey biomass (for alewife collected at Hamilton in 1972, we used average biomass values from Olcott, the closest port).

When grouping fish for analysis, we used fish length (subadult: ≤107 mm, adult: ≥108 mm), month (April–May (April 20 – May 11), June (2–14), July (July 19 – August 1), September (8–22), October (16–31)), and trawl depth (shallow: 9–34 m, intermediate: 35–69 m, deep: 70–146 m).

The diet of alewife was characterized by numbers and biomass of prey in stomachs. Percent occurrence of prey types was calculated as the percentage of alewife with nonempty stomachs containing a prey type. For both years, we estimated wet weight (grams) of alewife in April–May and October by use of length–weight regressions. The regressions were calculated from lengths and weights obtained each spring and fall from alewife collected soon after capture or after they were held on ice overnight. Wet weights for June–September were estimated by linear extrapolation between spring and fall values. We calculated the relative prey biomass, defined as the prey mass eaten per gram of fish, by dividing dry prey mass by the estimated wet weight of the fish. In addition, for each individual, we calculated the percentage of the prey weight contributed by each prey type. To examine patterns of microcrustacean zooplankton consumption between sites, we included only fish for which microcrustaceans made up at least 75% of the prey biomass and only alewife captured at shallow and intermediate depths to avoid bias due to the lack of samples from deep trawls at Rochester and Oswego in 1972. To determine how alewife size affected macroinvertebrate consumption, we pooled trawls for which occurrence of the particular macroinvertebrate was highest.

Results

1972

Stomachs of 490 adult alewife (≥108 mm) were examined; 460 contained identifiable prey, 10 contained unidentifiable

TABLE 1. Functional groupings of the prey of alewife in Lake Ontario during April–October in 1972 and 1988. Organisms were identified to the taxonomic level indicated, and those that were numerically important are marked with an asterisk.

1972	1988
Microcrustacean zooplankton	
Small cladocerans	Small cladocerans
Diaphanosoma sp.	*Eubosmina coregoni**
*Eubosmina coregoni**	*Bosmina longirostris**
*Bosmina longirostris**	*Chydorus sphaericus*
Chydorus sphaericus	*Ceriodaphnia lacustris*
Ceriodaphnia lacustris	
Large cladocerans	Large cladocerans
Daphnia sp.*	*Daphnia galeata mendotae*
Macrothricidae	*Daphnia retrocurva**
*Leptodora kindti**	*Daphnia pulex*
Holopedium gibberum	*Leptodora kindti*
Polyphemus pediculus	*Holopedium gibberum*
Ilyocryptus sp.	*Polyphemus pediculus*
	*Bythotrephes cederstroemi**
Calanoid/harpacticoid copepods	Calanoid/harpacticoid copepods
Harpacticoida*	Harpacticoida
Diaptomidae*	Diaptomidae*
*Limnocalanus macrurus**	*Limnocalanus macrurus**
*Eurytemora affinis**	*Eurytemora affinis**
Cyclopoid copepods	Cyclopoid copepods
*Diacyclops thomasi**	*Diacyclops thomasi**
Mesocyclops edax	*Acanthocyclops vernalis*
Tropocyclops prasinus mexicanus	*Mesocyclops edax*
	Tropocyclops prasinus mexicanus
Malacostracans	
*Mysis relicta**	*Mysis relicta**
Amphipoda*	Amphipoda*
Other prey	
Ostracoda	Ostracoda
Pisidium sp.	Rotifera
Hydrocarina	Coleoptera
Rotifera	Chironomidae*
Ascellus	Ephemeroptera
Bryozoa	
Mollusca	
Fish eggs	
Coleoptera	
Chironomidae*	
Ephemeroptera	

prey, and 20 were empty. Although we identified 31 food types in alewife stomachs (Table 1), only 12 items occurred frequently; they included nine species of microcrustacean zooplankton, *Mysis relicta*, amphipods, and chironomids.

Food habits of adult alewife

We grouped food of adult alewife into four prey types (zooplankton, mysids, amphipods, and other prey) and found that 73% of fish containing food consumed only one prey type (Table 2). Almost all alewife (91%) were eating one dominant prey type that contributed more than 75%, by weight, to their diet. Zooplankton and mysids were usually dominant prey types contributing the highest percentage of the weight in stomachs, amphipods were sometimes dominant but were more often sup-

TABLE 2. Numbers of adult alewife (out of 460 in 1972 and 611 in 1988) that ate mostly one prey type (100 or 75–99% of stomach contents by weight) in Lake Ontario during April–October in 1972 and 1988. Also shown is the mean percent of the weight in stomachs contributed by a prey type for alewife that ate that prey type.

Prey type	Weight in stomach 100%	Weight in stomach 75–99%	Mean percent of prey weight
1972			
Zooplankton	325	58	91
Mysis	4	16	86
Amphipods	4	8	42
Other[a]	2	2	18
Percent of all adults	73	18	
1988			
Zooplankton	338	42	77
Bythotrephes	14	58	62
Mysis	8	18	69
Amphipods	4	13	43
Other[a]	4	4	39
Percent of all adults	60	22	

[a] Insects, ostracods, fish eggs, bryozoans, and mites.

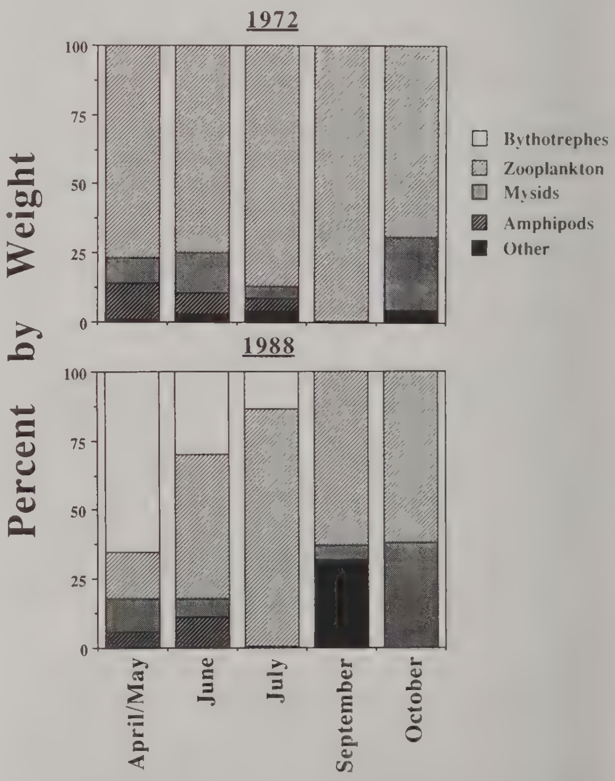

FIG. 2. Mean percent composition by weight contributed by *Bythotrephes* and other prey types to the diet of adult alewife in Lake Ontario, during April–October in 1972 and 1988 (one sample on August 1 included with July). Fish from all trawl hauls were pooled for each season; alewife in 1972 were captured off Hamilton, Rochester, and Oswego; alewife in 1988 were captured off Olcott, Rochester, and Oswego. The "other" category includes insects, ostracods, fish eggs, chironomids, bryozoans, and mites.

TABLE 3. Mean dry weight (mg) of prey eaten per gram wet weight of fish for adult alewife caught from Lake Ontario with bottom trawls in three depth ranges during April–October in 1972 and 1988. Also shown are the number of trawl hauls from which fish were examined and the number and mean total length of fish with identifiable prey in their stomachs.

Month	Trawl hauls (*N*)	Fish		Zooplankton					
		n	mm	*Bythotrephes*	Other	*Mysis*	Amphipods	Other[a]	Total
1972, shallow (9–34 m)									
April–May	3	18	162	0	0.05	0	0.01	<0.01	0.06
June	7	78	143	0	0.50	0	0	0.02	0.52
July	5	57	153	0	1.01	0	0.03	0.04	1.08
September	5	50	155	0	0.66	0	0.01	<0.01	0.67
October	3	27	153	0	0.28	0	<0.01	<0.01	0.28
1972, intermediate (35–69 m)									
April–May	3	31	153	0	0.07	0	0.01	<0.01	0.08
June	4	33	150	0	0.39	0.01	0	<0.01	0.40
July	3	17	148	0	0.70	0.02	0.01	0.03	0.76
September	3	16	162	0	0.47	0	0	0	0.47
October	4	39	159	0	0.26	0	<0.01	<0.01	0.26
1972, deep (70–146 m)									
April–May	3	22	155	0	0.01	0.58	0.09	0	0.68
June	2	15	171	0	0.11	1.44	0.25	0	1.82
July	1	9	144	0	0.27	0.05	<0.01	<0.01	0.32
September	2	20	144	0	1.00	0	0	0	1.00
October	1	10	173	0	0.05	1.01	<0.01	0	1.06
1988, shallow (9–34 m)									
April–May	0	0	—	—	—	—	—	—	—
June	3	32	156	0.66	0.71	0	0	0	1.37
July	4	77	159	0.14	0.78	0	0	0	0.92
September	1	18	135	0	0.03	0	0	0.04	0.07
October	0	0	—	—	—	—	—	—	—
1988, intermediate (35–69 m)									
April–May	3	38	156	0.84	0.42	0.12	0.01	<0.01	1.39
June	5	60	159	0.40	0.92	0.06	0.69	<0.01	2.09
July	5	85	160	0.09	0.75	0	0.01	<0.01	0.85
September	1	14	150	0	0.45	0.05	0.01	0.01	0.51
October	6	93	151	<0.01	0.79	0.01	<0.01	<0.01	0.80
1988, deep (70–146 m)									
April–May	6	82	151	1.07	0.06	0.21	0.20	0.01	1.54
June	1	13	160	0.47	1.23	0.39	<0.01	<0.01	2.09
July	0	0	—	—	—	—	—	—	—
September	0	0	—	—	—	—	—	—	—
October	3	50	149	<0.01	0.38	1.14	<0.01	<0.01	1.52

[a] Insects, ostracods, fish eggs, bryozoans, and mites.

plemental food, and other prey types were almost always supplemental.

Microcrustacean zooplankton dominated the diet of adult alewife during April–October, averaging 70% to nearly 100% of the mean percent composition of stomach contents by weight (Fig. 2). Nearly 30% of the diet of adult alewife by weight was *Mysis* in October, and 5–13% of the diet during April–August was amphipods.

Factors affecting alewife food habits

Depth — The most frequently observed prey items at shallow and intermediate depths from April through October were (in descending order) cyclopoid and calanoid copepods, small cladocerans, large cladocerans, and amphipods. Nearly 94% of all fish fed on cyclopoids during April–September, while calanoids were more frequent in the diet during April–July at shallow and intermediate depths. In contrast, large and small cladocerans became more important in the diet in late summer and fall. In terms of dry weight of prey eaten per gram of alewife, zooplankton dominated all other groups at shallow and intermediate depths (Table 3). The mean percent composition by weight of each prey type showed similar results, with zooplankton making up 80–100% of the diet (Fig. 2). For adults collected in deep water, the prey biomass consumed per gram of alewife was predominantly *Mysis* (April–June and October) and microcrustacean zooplankton (July and September).

Transect location — Zooplankton biomass consumed by adult alewife differed among sites (Table 4). Through July, cyclopoid copepods (mostly *Diaptomus thomasi*) were gener-

TABLE 4. Mean dry weight (mg) of zooplankton eaten per gram wet weight of adult alewife (>75% of stomach contents by weight) at bottom depths <70 m at different locations in Lake Ontario during April–October in 1972 and 1988.

Month	Fish (*n*)	Cladocerans[a]		Copepods		*Bythotrephes*	Total
		Large	Small	Calanoid	Cyclopoid		
			1972, Hamilton				
April–May	22	0	0	0.02	0.05	0	0.06
June	41	<0.01	<0.01	0.12	0.28	0	0.40
July	26	<0.01	0.01	0.10	0.96	0	1.07
September	20	0.55	0.05	0.01	0.45	0	1.06
October	29	0.27	0.01	0.05	0.15	0	0.48
			1972, Rochester				
April–May	0	—	—	—	—	—	—
June	39	0	<0.01	0.05	0.32	0	0.37
July	8	<0.01	0.01	<0.01	0.27	0	0.28
September	15	0.19	0.02	0.01	0.25	0	0.47
October	23	0.03	0.01	0.01	0.02	0	0.07
			1972, Oswego				
April–May	22	<0.01	<0.01	<0.01	0.05	0	0.06
June	21	<0.01	0.01	<0.01	1.29	0	1.30
July	30	0.03	0.11	0.03	0.99	0	1.16
September	30	0.30	0.01	0.01	0.08	0	0.39
October	9	0.10	0.06	<0.01	0.06	0	0.22
			1988, Olcott				
April–May	9	<0.01	<0.01	0.18	0.01	1.69	1.87
June	16	<0.01	0.01	0.03	0.44	0.48	0.97
July	59	0.01	0.02	0.01	0.60	0.25	0.89
September	0	—	—	—	—	—	—
October	37	1.32	0.01	0.08	0.17	<0.01	1.59
			1988, Rochester				
April–May	12	0	<0.01	0.04	0.11	0.38	0.53
June	34	<0.01	0.02	0.27	0.60	0.73	1.62
July	46	0.12	0.10	0.01	0.65	0.03	0.91
September	8	0.02	<0.01	0	<0.01	0	0.03
October	30	0.23	0.01	0.05	0.11	<0.01	0.39
			1988, Oswego				
April–May	14	<0.01	<0.01	0.31	0.56	0.72	1.60
June	29	<0.01	0.18	0.01	1.06	0.39	1.64
July	56	0.24	0.12	0.05	0.38	0.05	0.84
September	13	0.11	0.01	0.15	0.16	0	0.44
October	23	0.08	0.01	0.01	0.02	<0.01	0.11

[a] Species listed in Table 1.

ally the dominant zooplankton in alewife stomachs at depths <70 m at all sites. Small cladocerans (mostly bosminids) and large cladocerans (daphnids and *Leptodora kindti*) first became important in the diet at Oswego in July and at Rochester and Hamilton in September. At Oswego, microzooplankton biomass eaten was highest in June and declined steadily through October; at Hamilton, the contribution was highest in July and September, and at Rochester there was no clear peak and the microcrustacean biomass consumed per gram of fish was lower than at other transects.

Alewife size — To determine if larger adult alewife preyed more heavily on large cladocerans than did smaller adult alewife, we summarized *Leptodora kindti* consumption for three trawls (18, 27, and 46 m) made at Oswego on September 7, 1972. *Leptodora kindti* were eaten by 31 of 32 adult alewife examined from these trawls. The 31 alewife ranged in length from 140 to 185 mm. They were grouped into five 10-mm length groups, and mean number of *Leptodora* eaten increased with fish length ($r = 0.88$, $n = 31$, $P = 0.001$). On average, alewife 140–149 mm had eaten 300 *Leptodora* whereas those 180–189 mm had eaten nearly 600.

1988

Twenty-six food items were identified in alewife stomachs in 1988, 11 of which were numerically important, including *Bythotrephes cederstroemi* (Table 1). Prey that were numerically important in 1972 were usually also numerically important in 1988. Zooplankters netted from the lake in 1988, however, did not include *Bythotrephes*. Exclusive of nauplii, 80–87% of the Lake Ontario zooplankton community during

April–October was *Diacyclops thomasi*, *Leptodiaptomus minutus*, *Acanthocyclops vernalis*, *Daphnia retrocurva*, and *Bosmina longirostris*. In 1987, *Bythotrephes* was found only in those zooplankton samples taken in October (densities at inshore and offshore sites were <1/L).

Food habits of adult and subadult alewife

Of 611 adult alewife examined, three contained unidentifiable prey and 46 were empty. Adult alewife usually ate only one prey type and almost always (82%) ate one dominant food type that contributed at least 75% of the fish's prey by weight (Table 2). As in 1972, zooplankton and *Mysis* were the dominant foods that contributed the highest percentage of the weight in stomachs. The third-highest contributer was *Bythotrephes*. Amphipods and other prey remained of secondary importance.

In 1988, *Bythotrephes* dominated the food of adult alewife by weight in April–May and declined after August (Fig. 2). This large cladoceran was no longer in alewife guts in September and October, at which time 30% or more of the diet of these fish was mysids and chironomids. Apparently alewife were able to find *Bythotrephes* in Lake Ontario in 1988, even though they were not abundant enough to be in our zooplankton samples.

Subadult alewife (150 examined) fed almost exclusively on microcrustacean zooplankton (Table 5). Of 125 subadult alewife with identifiable food, only one had eaten an amphiphod and six had eaten chironomid larvae or pupae. *Bythotrephes* occurred in 8 of 31 subadult alewife in April–May and 5 of 56 subadults in June. The smallest alewife that ate *Bythotrephes* was 75 mm; all others were ≥91 mm.

Factors affecting alewife food habits

Depth — Microcrustacean zooplankton (cyclopoid and calanoid copepods, small and large cladocerans, and *Bythotrephes*, in that order) were numerically dominant in the diet of adult alewife collected at shallow and intermediate depths throughout 1988. An exception was the alewife from a single trawl made in shallow waters in September, when the main food item was chironomids. For fish taken from deep water, cyclopoid and calanoid copepods, small cladocerans, *Bythotrephes*, and other large cladocerans occurred most often in alewife stomachs, in that order.

Microzooplankton, including *Bythotrephes*, dominated the biomass eaten per gram of alewife at all depths during April–June (Table 3). Thereafter, zooplankton other than *Bythotrephes* usually dominated at shallow and intermediate depths; *Bythotrephes* was a minor part of the biomass eaten in July and contributed virutally nothing in September–October. In deep water, *Mysis* accounted for most of the dry weight of prey eaten in October (Table 3), even though more fish ate microzooplankton.

To examine how *Bythotrephes* was incorporated into adult alewife diets, we performed chi-square tests on pooled data from 12 trawls (April–May and June, intermediate and deep trawls). *Mysis* and non-*Bythotrephes* zooplankton were usually not found together in the same fish ($P < 0.01$), possibly because the feeding modes for fish eating macro- and microzooplankton are different. Alewife were probably particulate-feeding on *Bythotrephes* because the presence of *Bythotrephes* in alewife stomachs was independent of the presence of *Mysis* ($P = 0.97$) and of the presence of non-*Bythotrephes* microzooplankton ($P = 0.52$).

Transect location — As in 1972, zooplankton biomass consumed per gram of alewife differed seasonally among sites (Tables 4 and 5). Considering only non-*Bythotrephes* biomass eaten by adult alewife, zooplanktivory at Oswego peaked in June and declined through October. At Rochester, zooplanktivory was highest in June and July whereas at Olcott, it was highest in October. Cyclopoid copepods were the dominant non-*Bythotrephes* microcrustaceans eaten by adults and subadults at all sites through June and at Rochester in July; small cladocer-

TABLE 5. Mean dry weight (mg) of prey eaten per gram wet weight of fish for subadult alewife caught from Lake Ontario with bottom trawls at three locations during April–October 1988. Also shown are the number of trawl hauls from which fish were examined and the number and mean total length of fish with identifiable prey in their stomachs.

	Trawl hauls	Fish			Cladocerans[a]		Copepods			
Month	(*n*)	*n*	mm	*Bythotrephes*	Small	Large	Cyclopoid	Calanoid	Harpacticoid	Other[b]
					Olcott					
April–May	3	5	89	0.33	0	0	0.05	0	0	0
June	3	27	92	0.09	<0.01	0.01	0.32	0.03	<0.01	<0.01
July	0	0	—	—	—	—	—	—	—	—
September	0	0	—	—	—	—	—	—	—	—
October	2	2	98	0	<0.01	0.41	0.02	0.19	0	0
					Rochester					
April–May	3	10	82	0.02	0	0	0.27	0.07	0	0
June	3	17	89	0.06	0.01	<0.01	1.58	0.46	0	0.10
July	1	12	99	0	0.23	0.09	0.59	<0.01	0	0
September	0	0	—	—	—	—	—	—	—	—
October	2	7	91	0	0.01	0.50	0.37	0.12	0	0
					Oswego					
April–May	3	16	89	0.46	<0.01	0	0.93	0.50	0	0
June	3	12	92	0.12	0.19	0.01	1.60	0.04	<0.01	0
July	1	2	92	0	0.23	0.13	0.27	<0.01	0	0
September	1	2	85	0	<0.01	0.05	0.05	<0.01	0	0.02
October	3	13	78	0	0.10	0.32	0.23	0.06	0	0

[a] Species listed in Table 1.

[b] Amphipods and chironomids.

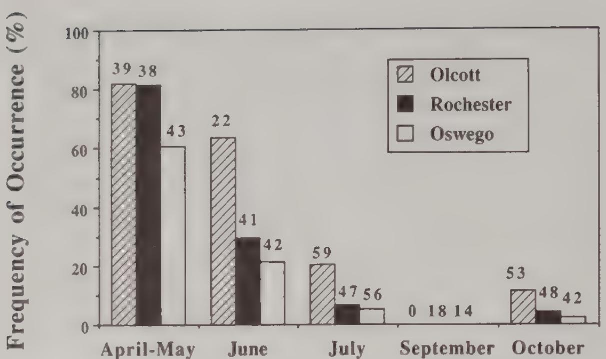

FIG. 3. Frequency of occurrence of *Bythotrephes cederstroemi* in stomachs of adult alewife at three locations in Lake Ontario during April–October 1988. Number of fish examined is above each bar.

ans became secondarily important at Oswego in June and at Rochester in July (Tables 4 and 5). Large cladocerans were the dominant prey of subadult fish at all sites in October.

Percent frequency of occurrence of *Bythotrephes* in adult alewife stomachs was consistently highest at Olcott, intermediate at Rochester, and lowest at Oswego (Fig. 3). However, the relative biomass of *Bythotrephes* eaten by alewife did not follow this site-to-site pattern through the season (Table 4). It was usually highest at Olcott, but the ranking differed by date at Rochester and Oswego.

Alewife size — To determine if alewife size was an important factor in the consumption of *Mysis*, amphipods, and *Bythotrephes*, we examined data from trawls where they were frequently eaten (Fig. 4). For seven deep trawls in April where *Mysis* were common prey, fish <130 mm did not eat *Mysis*. Amphipods were consumed by 44 of 74 fish taken from five trawls (June) where their percent occurrence in fish stomachs was 50% or greater. Fish <130 mm rarely ate amphipods; occurrence and median number consumed increased with fish length and were highest for the largest fish examined (160–169 mm). For *Bythotrephes*, we pooled 18 trawls made in April–May and June and found that this organism occurred in 50% of fish 90–109 mm (subadults) and in about 70% of fish >110 mm. In general, the number of *Mysis* and *Bythotrephes* eaten increased with fish size and *Bythotrephes* was eaten by fish as small as 75 mm.

Alewife Abundance, Size, and Condition in 1972 and 1988

Abundance of adult alewife in 1972 was similar to that in 1988 (ANOVA of $\log_{10}$-transformed trawl catches, $P = 0.33$) whereas abundance of subadult alewife in 1972 was lower than in 1988 ($P = 0.03$). Although adult alewife numbers were similar in both years, the fish were smaller in 1972 (Kolmogorov–Smirnoff test, $P < 0.01$). The modal length group in 1972 was 140–149 mm, and 15% of the adults were ≥165 mm whereas in 1988 the modal group was 160–169 mm, and 21% of the adults were ≥165 mm. Lengths of subadults were not different ($P = 0.75$), although the small number measured in 1972 (32) precluded detection of all but the grossest of differences.

In 1988, abundance of adult alewife differed in the three lake areas we sampled. During April–June, catches of adults increased from Olcott eastward to Oswego (Table 6). After June, the west-to-east gradient in abundance disappeared, and the fish were equally abundant at Olcott and Oswego. At Rochester, adult abundance was variable after June and not similar to that in the other two lake areas.

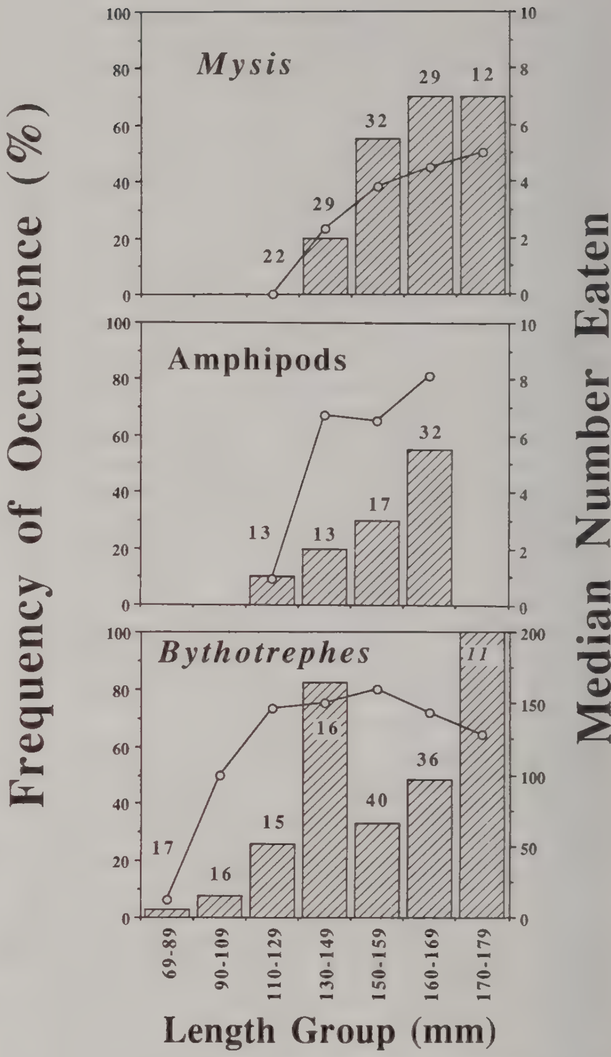

FIG. 4. For alewife caught where *Bythotrephes cederstroemi*, *Mysis relicta*, and amphipods were frequently eaten, the frequency of occurrence (line) of the three prey in alewife stomachs and the median number eaten (bar) by alewife in various length groups in Lake Ontario during April–October 1988. Number of fish examined is above each bar.

The slope of the length–weight relationship for adult alewife in spring 1972 was not as steep as the slope of the length–weight relationship in spring 1988 (ANCOVA, test for homogeneity of slopes, $P < 0.01$). The two regression lines intersected when alewife length exceeded 164 mm, so, on average, fish ≤165 mm were heavier in 1972, and those ≥165 mm were heavier in 1988. In fall, slopes of length–weight relationships for alewife 150–179 mm were similar ($P = 0.78$), but a significantly higher intercept in 1972 (ANCOVA, $P < 0.01$) indicated that the condition of the fish that fall was better than in fall 1988.

Discussion

Our findings indicate that colonization of Lake Ontario by *Bythotrephes* has led to a shift in the feeding ecology of the

TABLE 6. Mean numbers of adult alewife (antilogged means of the average $\log_{10}$-transformed catches) caught per 10-min tow with a bottom trawl in three areas of Lake Ontario during four sampling periods in 1988. For each sampling period, P values are from ANOVA performed with a general linear model on the $\log_{10}$-transformed catches, and means followed by the same letter are not significantly different (Tukey–Kramer multiple comparison test, $P < 0.05$).

	Sampling period			
Area	April–May	June	July	October
Olcott	148 z	134 z	57 z	49 z
(*n*)	(23)	(17)	(19)	(17)
Rochester	484 z	409 z y	11	249
(*n*)	(23)	(18)	(13)	(15)
Oswego	901 z	748 y	70 z	16 z
(*n*)	(27)	(14)	(17)	(20)
P	0.074	0.056	0.022	0.002

alewife. The shift, however, was not as we expected from macrozoobenthos to zooplankton, but rather the shift was within the zooplankton community. Benthic macroinvertebrates were as important in the April–October diet of alewife in Lake Ontario in 1988 as they were in 1972. *Mysis* and amphipods combined made up about 25% of the diet (wet weight) in spring and fall but <10% in summer. Zooplankton made up the bulk of the diet in both years, but in spring 1988, the exotic cladoceran *Bythotrephes cederstroemi* was the most frequently eaten microcrustacean, contributing >60% of the food by weight. *Bythotrephes*, most likely because of its large size and visibility, was actively preyed on by adult and larger subadult alewife, and if it becomes premanently abundant in Lake Ontario, alewife would have a greater reliance on this organism than we demonstrated in this study.

Although *Bythotrephes* was first reported from the southwestern region of Lake Ontario in 1985, it was absent from plankton samples collected in other lake areas until fall 1987 (Makarewicz and Jones 1990; Johannsson and O'Gorman 1991; Johannsson et al. 1991; this study). *Bythotrephes* was not in plankton collections in 1988, yet we found them in abundance in the stomachs of alewife, leading us to conclude that alewife seek out these prey even if densities and encounter rates are low. Johannsson et al. (1991) attributed the abundance of *Bythotrephes* in 1987 to reduced alewife predation because numbers of adult alewife in spring 1987 were the lowest of any spring during 1985–88. But in spring 1990, adult abundance was equally low, and *Bythotrephes* failed to reappear (E. L. Mills and R. O'Gorman, pers. obs.). Perhaps a reduction in predation pressure for more than one summer is needed for substantial *Bythotrephes* recruitment to develop. (There is some evidence that the decline in alewife numbers noted in spring 1987 began in late summer 1986 whereas the downturn noted in spring 1990 most likely occurred in winter 1989–90.) Or perhaps unusually rapid warming of the lake in 1987 (Johannsson et al. 1991) worked in concert with reduced predation pressure and allowed a population to develop. In any event, if alewife numbers in Lake Ontario decline well below 1985–88 levels, *Bythotrephes* could redevelop, and alewife again would shift to feeding on it.

In Lake Ontario, tailspines were typically the only body part of *Bythotrephes* in alewife stomachs, and they were frequently found in a large bolus. Retention time for tailspines is unknown, but if it is longer than that for the body parts of other plankters, our estimates of importance of *Bythotrephes* to the diet of alewife may be exaggerated (Gannon 1976). For example, the seasonal cycle of *Bythotrephes* in European lakes indicates that, in general, this zooplankter is rare in early spring (Sprules et al. 1990), yet we encountered the most spines in stomachs in April–May. We doubt that the spines were retained for months in alewife stomachs, even at the low water temperatures of winter, but we cannot completely eliminate that possibility. Alewife may also have been feeding on the spines of dead *Bythotrephes* that had settled to near bottom, or perhaps this organism concentrated near bottom. Evans (1988) found tailspines in the stomachs of deepwater sculpin (*Myoxocephalus thompsoni*) collected with bottom trawls at 91 m in Lake Michigan, and she hypothesized that the benthic sculpins were eating dead (and dying) *Bythotrephes*.

Incidence of *Bythotrephes* in alewife stomachs and its occurrence in the diet indicated a west-to-east gradient along the south shore of Lake Ontario during 1988. Its contribution to the alewife's diet declined from Olcott (nearest the Niagara River) to Oswego, indicating that abundance was highest in areas closest to the Niagara River. During April–June, this was probably due to differences in predation pressure as alewife numbers increased from Olcott eastward to Oswego. O'Gorman et al. (1991) demonstrated that spatial concentration of alewife in Lake Ontario can reduce the abundance of the largest zooplankters in a lake area. During July–October, there was no gradient in alewife numbers along the south shore, and we suspect that the gradient in *Bythotrephes* abundance was due to considerable numbers of them entering Lake Ontario from Lake Erie via the Niagara River. Of all the Great Lakes, Lake Erie appears to have the highest lakewide population of *Bythotrephes* (Jin and Sprules 1990), and abundance there usually peaks in summer and fall (J. H. Leach, OMNR, R.R. 2, Wheatley, Ont. N0P 2P0, pers. comm.).

As alewife grow longer, they eat larger prey items such as *Leptodora* and *Bythotrephes* more frequently and in greater numbers. Therefore, despite similar numbers of adults in 1972 and 1988, predation pressure on large zooplankters was greater in 1988 because adult alewife were longer in 1988 than in 1972. If the size structure of adult alewife in 1988 had been similar to that in 1972, *Bythotrephes* would have persisted longer in the lake and in the fish's diet. The notion that alewife size structure is one of the important determinants for establishment of populations of large cladocerans in Lake Ontario was first suggested by Johannsson et al. (1991). They showed that the dates when four species of large cladocerans first appeared in midlake during 1981–88 were more strongly correlated with the abundance of alewife ≥165 mm ($r = 0.84$) than they were with cumulative epilimnetic temperature ($r = -0.63$).

The ability of the longest alewife to eat large quantities of *Bythotrephes* and the availability of *Bythotrephes* from fall 1987 through spring 1988 may have been the reasons, in part, that the slope of the length–weight relationship for adult alewife in spring 1988 differed from that in spring 1972. In Lake Ontario, the slope of the length–weight relationship for adult alewife in spring is correlated with the number of adults caught (for 1978–90, excluding 1988: $r = -0.82$, $P < 0.01$; R. O'Gorman, unpubl. data). Yet, even though adult catches were similar in 1972 and 1988, the slopes of the length–weight relationships differed because alewife ≥165 mm were heavier in 1988. Furthermore, they were heavier even though they were more abundant, which indicates that the longest adults had access to more food resources in 1988 than they did in 1972. After spring, the contribution of *Bythotrephes* to the diet declined rapidly, and in fall, the slopes of the length–weight relationships were similar, although the fish were lighter in 1988. This disparity was probably due to the much greater abundance of yearling alewife in 1988 and the resultant heavier predation pressure they exerted on the zooplankton community in summer and fall 1988.

Previous studies of alewife feeding have indicated that the diet is strongly influenced by lake thermal structure (Brandt 1980; Brandt et al. 1980; Janssen and Brandt 1980). Adult alewife are adept pelagic planktivores, particle-feeding on macrozooplankton as well as filter-feeding on microzooplankton, but are poor benthic feeders (Janssen 1976, 1978, 1980). Availability of benthic macroinvertebrates is seasonally variable and dependent on temporal and spatial overlap of predator and prey. Amphipods become active off bottom primarily during spring (Wells 1968). *Mysis relicta* prefers temperatures <6°C; it migrates inshore during winter and, as summer warming progresses, moves offshore, where it makes diurnal migrations from the lake bottom to the base of the thermocline (Beeton 1960; McNaught and Hasler 1966; Robertson et al. 1968; Carpenter et al. 1974; Balcer et al. 1984). In 1972 and 1988 in southern Lake Ontario, some alewife ate macroinvertebrates in spring, before a thermocline was firmly established, and in fall, as the thermocline underwent erosion. During the period of strong thermal stratification, the majority of alewife are epilimnetic (Olson et al. 1988; Elrod and O'Gorman 1991; Johannsson and O'Gorman 1991), and during this period, adult and subadult alewife in southern Lake Ontario fed on microcrustacean zooplankton.

Feeding habits of alewife appear to differ among Great Lakes populations. Modeling of alewife planktivory in Lake Michigan by Hewett and Stewart (1989) assumed that *Mysis* and *Pontoporeia* combined made up 25–45% of the adult diet (by weight) in summer and 0–25% of the yearling diet. Our results indicate that alewife use of high-energy macroinvertebrate prey is much lower in Lake Ontario, especially during thermal stratification. Predation pressure on the microzooplankton community, as well as consumption of microzooplankton by different age-classes of alewife and other fishes, is much higher in southern Lake Ontario than that predicted in Lake Michigan. In western Lake Ontario, however, where upwelling of cold bottom water is common and the thermocline is less firmly established, larger alewife may not always be separated from macrozooplankton by a strong thermal barrier during summer and fall. Alewife collected at Hamilton (western Lake Ontario) in 1972 seem to support this motion; they consumed *Mysis* as late as July. Consequently, because inter- and intralake differences in diet clearly exist, they must be incorporated into models of alewife planktivory to gain an accurate understanding of energy flow between trophic levels in each of the Great Lakes.

Microcrustacean zooplankton are low in caloric density relative to amphipods and mysids (Stewart and Binkowski 1986), but particle size is an important determinant of passage rate and digestibility; small particles such as microzooplankton have a much greater surface-to-volume ratio, so they digest rapidly. Bioenergetic models of alewife feeding have neglected the effect of particle size (e.g. Stewart and Binkowski 1986; Hewett and Stewart 1989), but this factor may provide a mechanism for optimizing foraging efficiency in order to maximize digestible-energy intake. If true, increased surface-to-volume ratio and passage rate of microzooplankton may allow alewife to compensate for their relatively lower energy content.

The patchy distribution of alewife and the fact that alewife were not collected synoptically could influence interpretation of site-to-site differences in planktivory. For example, fall collections in 1988 were made first at the westernmost sites and up to 2 wk later at Oswego. Zooplankton abundance in Lake Ontario can change rapidly (Johannsson 1987), and spatially concentrated alewife can change the size structure of the zooplankton community (O'Gorman et al. 1991). During our study, however, some of the seasonal site-to-site differences, in microzooplanktivory appear to reflect different rates of zooplankton community development that are due to east-to-west temperature gradients in Lake Ontario (Patalas 1969, 1972; Johannsson 1987). In late spring or early summer, after the disappearance of the thermal bar (Rodgers 1965, 1987), prevailing northwesterly winds push warm surface water to the east, resulting in the earlier appearance of most species in the east, and a higher density of zooplankton in the eastern part of the lake in early to midsummer, declining by fall (Patalas 1969). Alewife zooplanktivory at Oswego reflected this seasonal pattern in 1972 and 1988. Czaika (1974) studied the nearshore zooplankton community in southwestern Lake Ontario from Port Weller to Rochester in 1972 and found that the density of most species peaked in September and October. In this study, alewife microzooplanktivory at Hamilton was higher than at Rochester or Oswego in September and October 1972 whereas in October 1988, microzooplanktivory was highest at Olcott. Differences in alewife abundance in different areas of the lake might also be expected to influence zooplankton density and thus zooplanktivory as reflected in the stomach contents. But in 1988 at least, alewife were not consistently concentrated in any lake area after spring, so site-to-site differences in microzooplanktivory were probably due to varying rates of zooplankton community development along the south shore.

Our results indicate that during summer and early fall, adult alewife prey wholly on microzooplankton, thus competing with subadults during the growing season. Although larger alewife are more likely to consume larger species of zooplankton such as *Leptodora kindti* and to retain larger plankters in general (MacNeill and Brandt 1990), there is considerable overlap in the sizes of zooplankton that are consumed by different life stages (O'Gorman et al. 1991). Competition for zooplankton food resources among adult, yearling, and young-of-year alewife is a strong possibility and probably influences alewife population dynamics (O'Gorman et al. 1987). Recent studies have indicated that the Lake Ontario zooplankton community has remained stable from the late 1960's to the mid-1980's (Johannsson 1987) despite decreased nutrient loading (Stevens and Neilson 1987) and increased stocking of salmonine predators (O'Gorman et al. 1987). Given the demonstrated dependence of all ages of alewife on microcrustacean zooplankton, continued reductions in nutrient loading and other factors that lower phytoplankton and zooplankton production will have a significant effect on both the alewife community and the salmonine population it supports.

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Variable Natural Mortality Rates Inflate Variance of Recruitments Estimated from Virtual Population Analysis (VPA)

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We used a simulation model to determine whether estimates of fish recruitment obtained from virtual population analysis (VPA) (1) have the correct interannual variability and (2) yield high statistical power (>0.8) when correlated with an environmental factor, given that the "true" instantaneous adult natural mortality rate (M) likely varies over time but a constant M is used in VPA (M^{VPA}). Under such circumstances, VPA exaggerates variability in recruitment, which reduces the probability of correctly detecting environmental correlates with recruitment. The magnitude of these effects increases with increases in (1) the absolute value of the true mean M, (2) the variation in M over time, (3) the relative error in M^{VPA}, and (4) the magnitude of M^{VPA} relative to F_L (instantaneous terminal fishing mortality rate) and decreases with increases in magnitude of the true variation of recruitment or the true correlation with the environmental factor (all else being equal). This bias is not large under most conditions, but it is likely to be more important in short-lived, high-M species than the similar but counteracting bias caused by aging errors. Sensitivity analyses can demonstrate how various M^{VPA} values affect conclusions about environmental correlates with recruitment.

Nous avons appliqué un modèle de simulation à la détermination de deux caractéristiques des estimations du recrutement de poissons obtenues par analyse des populations virtuelles (APV) : 1) la variabilité d'une année à l'autre de ces estimations est-elle correcte et 2) ces estimations sont-elles puissantes ($>0,8$) lorsqu'elles sont mises en corrélation avec un facteur écologique, compte tenu du fait que le taux "réel" instantané de mortalité naturelle (M) chez les adultes est sujet à varier en fonction du temps, alors qu'un taux M constant est appliqué dans l'APV (M^{APV})? Dans ces conditions, l'APV accentue la variabilité du recrutement, ce qui réduit la probabilité de la détection correcte de corrélations entre le recrutement et des facteurs écologiques. L'importance de ces effets s'accroît à mesure que s'accroissent : 1) la valeur absolue de la moyenne vraie M; 2) la variation de M en fonction du temps; 3) l'erreur relative de M^{APV} et 4) la grandeur de M^{APV} relativement à F_L (taux instantané de mortalité par pêche en estuaire). L'importance de ces effets diminue avec l'accroissement de la variation vraie du recrutement ou de la corrélation vraie avec le facteur écologique (toutes autres choses étant égales). La plupart du temps, cette erreur systématique est peu importante, mais elle risque de l'être davantage chez les espèces à courte durée de vie et à forte M, que ne l'est l'erreur systématique qui fait contrepartie, c'est-à-dire celle attribuable à des erreurs dans l'évaluation de l'âge. Des analyses de sensibilité peuvent montrer de quelle manière les différentes valeurs prises par M^{APV} modifient les conclusions relatives aux facteurs écologiques mis en corrélation avec le recrutement.

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Most studies attempting to identify causal mechanisms behind the variability in abundance of fish surviving to recruit have used recruitment indices estimated by virtual population analysis (VPA). Estimates from VPA are often favored over alternative indices of recruitment for at least two reasons (Shepherd et al. 1984). Reasonably long age-structured data series of catches are available for many species relative to research trawl surveys, and other indices such as catch per unit of effort (CPUE) may be confounded by changes in catchability.

For VPA estimates to provide an appropriate index of recruitment, it is critical that they have the correct temporal pattern of abundances. However, many studies have shown that recruitment estimates from VPA may be biased (Pope 1972; Agger et al. 1973; Ulltang 1977; Sims 1982, 1984; Rivard and Foy 1987; Rivard 1989) or may contain spurious time trends (Rivard 1983; Hilden 1988; Bradford and Peterman 1989; Lapointe et al. 1989). Such spurious time trends in estimates of recruits obtained from VPA can cause incorrect conclusions about correlations with environmental factors (Lapointe and Peterman 1991).

In addition, other studies have documented that the variance of VPA recruitment estimates may also be biased in certain situations. First, aging errors may lead to underestimates of both recruitment variability and correlations between recruitment and environmental factors, even if VPA is given correct values of natural and fishing mortality rates (M and F) (Rivard 1989; Bradford 1991). Second, the variance of VPA recruitment estimates depends on both the natural variability and uncertainty of inputs to VPA (i.e. catches, M, and F; Pope 1972; Pope and Garrod 1975; Pope and Gray 1983; Saila et al. 1985; Brander 1987; Sampson 1987, 1988; Kimura 1989). Thus, if VPA input parameters are estimated with error, the variance of recruitment estimates may be biased. One example of this arises because most analysts are forced to assume that M is constant through time in VPA reconstructions. If M is variable among years in nature because of varying abundance of predators or other factors (e.g. Pope and Knights 1982; Daan 1987; see Vetter 1988 for a review), an assumed constant M will be incorrect by various amounts in different years. Because VPA's reconstruction procedure inflates abundance estimates by the natural and fishing mortality rates, abundance estimates will also be inaccurate by varying amounts in different years. Ulltang (1977) found that the highest relative error in estimates of total stock size was only 6% when a constant M of 0.2 was used in VPA but the true M varied between 0.1 and 0.3. But Hilden (1988) stated that under similar conditions, VPA estimates may exaggerate recruitment fluctuations and that this property may explain the difficulty in relating recruitment data to series of environmental variables. However, neither Ulltang (1977) nor Hilden (1988) quantified the effect of the assumption of constant M on either the estimated variability of recruitment or the potential to detect environmental correlates with recruits.

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We elaborate upon Hilden's suggestions by first quantifying the effect on the estimated interannual variability in recruits of assuming a constant M in VPA (denoted by M^{VPA}) when the true M (denoted by M) varies temporally. To determine how sensitive correlations between environmental variables and recruitment might be to the assumption of a constant M^{VPA}, we then calculate the effect of this assumption on statistical power, the probability of correctly detecting correlations between the abundance of recruits and environmental factors. Finally, we examine the sensitivity of our results to various levels of interannual variation in M derived from the literature and for a range of possible true correlations in nature.

Methods

We simulated an age-structured fish population with variable M to generate the true interannual variability in recruitment and the true correlation coefficient between recruits and an environmental factor. By simulating known situations and performing VPAs and correlation analyses on the resulting data, we were able to quantify the magnitude of bias caused by assuming a constant annual M^{VPA} and to identify the causes of that bias. Each simulation proceeded as follows.

First, to make our results generally applicable to a variety of situations in which recruitment variation is caused by different mechanisms, we used the following general equation to generate values of true recruits and an environmental factor that varied randomly over time and were positively correlated:

$$(1)\quad Y_t = kE_t + \sqrt{(1-k^2)}v_t$$

where Y_t is $\log_e$(recruits) in year t, E_t is the environmental factor, k is a constant, and v_t is an error term. E_t and v_t are independent and normally distributed with mean 0 and variance of 1. Under these conditions, it can be shown from the definition of a correlation coefficient that equation 1 generates Y_t values with mean 0 and variance of 1 and a correlation coefficient (ρ) between Y_t and E_t with a mean equal to k (i.e. $\rho = k$).

TABLE 1. Parameter values for three hypothetical fish stocks. Shown are the mean instantaneous annual natural mortality rate ($\bar{M}$), the number of ages (A), and the age-specific selection coefficients (s_i).

	Low-M stock	Medium-M stock	High-M stock
$\bar{M}$	0.2	0.5	1.0
A	10	7	5
	Age-specific selection coefficients (s_i)		
Age			
1	0.5	0.5	0.5
2	0.7	0.7	1.0
3	0.9	1.0	1.0
4	1.0	1.0	1.0
5	1.0	1.0	1.0
6	1.0	1.0	—
7	1.0	1.0	—
8	1.0	—	—
9	1.0	—	—
10	1.0	—	—

We let E_t represent a standardized environmental variable and scaled Y_t to a mean of 14 and standard deviation of $\log_e$(recruits), SD_N, of 0.3 based on values reported for fish stocks by Hennemuth et al. (1980). The raw number of recruits in each year t ($N_{1,t}$) was calculated from

$$(2)\quad N_{1,t} = e^{Y'_t}$$

where Y'_t is a scaled value of $\log_e$(recruits) in year t (i.e. $Y'_t = \text{SD}_N Y_t + \text{mean}$). Thus, raw recruits varied randomly according to a lognormal distribution and had a coefficient of variation (CV) of approximately 31%. For our initial simulations, we used $k = 0.7$. In addition, to determine the sensitivity of the results to different assumed true correlations, separate simulations were performed with k ranging from 0.4 to 0.9.

Numbers of fish in older age classes were generated by

$$(3)\quad N_{i+1} = N_i e^{-Z_i}$$

where N_i is the number of fish of age i and $Z_i = M_t + F_i$. M_t was chosen randomly from a normal distribution with true mean $\bar{M}$ and standard deviation SD_M. We calculated F_i, the instantaneous age-specific fishing mortality rate, from

$$(4)\quad F_i = s_i F_L$$

where the s_i values are the age-specific selection coefficients and L denotes the last (i.e. oldest) age class. To simulate a reasonably sustainable level of fishing mortality for each type of fish stock, we set $F_L = 0.5\bar{M}$ for each year. We relaxed this assumption of constant F_L in sensitivity analyses below. We quantified the effects of failing to account for a variable M for three hypothetical stocks with different $\bar{M}$ values, s_i values, and numbers of ages to represent a range of stock types (e.g. long-lived groundfish, short-lived pelagic clupeoids; Table 1). For each hypothetical stock, we performed separate simulations using one of a range of SD_M values that represented coefficients of variation in M [CV(M)] of 0–40%. We use the phrase "variation in adult M" below to avoid confusion with variation in prerecruit mortality (modeled implicitly by equations 1 and 2); the latter is not part of VPA's estimation. But note that "variation in adult M" specifically applies to M for fished age classes and therefore may apply to immature or juvenile fish if they are harvested. Thus, for example, the maximum for our range of CV(M) is consistent with that estimated due to variability in

TABLE 2. Results of simulations for the medium-M stock with mean correlation between true recruits and the environmental variable of 0.7 and $M^{\mathrm{VPA}} = \bar{M}$. Shown are the standard deviation of M (SD_M), the coefficient of variation of M (CV(M)), the mean true and estimated $\log_e$(recruits), the mean correlation between estimated $\log_e$(recruits) (R_{est}) and true $\log_e$(recruits) (R_{true}), the average true and estimated standard deviation (SD) of $\log_e$(recruits), the percent difference between standard deviations of the true time series of $\log_e$(recruits) and the time series estimated by VPA [100 × (estimated − true)/true; % diff. SD], the mean correlation between estimated $\log_e$(recruits) (R_{est}) and the environmental factor, and the power to detect a significant correlation between estimated recruits and the environmental factor.

		Mean [$\log_e$(recruits)]		Mean $\hat{r}$ between R_{est} and R_{true}	SD[$\log_e$(recruits)]			Mean $\hat{r}$ between R_{est} and environmental factor	
SD_M	CV(M)(%)	True	Estimated		True	Estimated	% diff. SD		Power
0.0	0	14.00	14.00	1.00	0.296	0.296	0.0	0.704	1.00
0.025	5	14.00	14.00	0.99	0.296	0.298	0.6	0.699	0.99
0.050	10	14.00	14.00	0.98	0.296	0.304	2.6	0.685	0.97
0.075	15	14.00	14.00	0.95	0.296	0.314	5.9	0.665	0.95
0.100	20	14.00	14.01	0.92	0.296	0.327	10.3	0.640	0.91
0.125	25	14.00	14.01	0.88	0.296	0.343	15.7	0.612	0.87
0.150	30	14.00	14.02	0.84	0.296	0.362	22.0	0.582	0.81
0.175	35	14.00	14.02	0.80	0.296	0.382	29.0	0.553	0.75
0.200	40	14.00	14.03	0.76	0.296	0.405	36.7	0.524	0.68

predation mortality alone for young fished age classes of some North Sea stocks (Daan 1987; Hilden 1988).

The Baranov catch equation (Ricker 1975) was used to generate catches:

$$(5)\quad C_i = \frac{N_i F_i (1 - e^{-Z_i})}{Z_i}$$

where C_i is the number of fish caught at age i.

Estimated Populations

The model estimated populations using the standard formulation for exact VPA (Gulland 1983, p. 105). Details of notation and procedure are given in Lapointe et al. (1989). Catch data were generated for 30 yr to ensure that estimates of recruits in the last year were derived from cohorts that had reached the oldest fished age. Thus, our calculations of the variance of recruits and power described below only used recruits from years 1–20 that were estimated from "complete" cohorts. In each simulation, we gave VPA the true s_i vector and the true time series of simulated catches and F_L values. However, VPA was given an incorrect and constant M^{VPA}. We explored two qualitatively distinct cases of incorrect M^{VPA} values: (1) a constant M^{VPA} equal to the true $\bar{M}$ and (2) an incorrect and constant M^{VPA} equal to the true $\bar{M}$ plus (or minus) 50%.

Calculation of Variance of Recruits and Power

The variance in estimated and true recruits among years was calculated using the standard formula for sample variance (Zar 1974). Calculations of variances and correlations with the environmental factors used $\log_e$-transformed recruits.

For each of 1000 Monte Carlo trials, we estimated power, the probability of correctly concluding that there was significant positive true correlation between recruitment and an environmental variable in nature. First, we calculated product-moment correlation coefficients ($\hat{r}$ values) between each 20-yr time series of recruitment and the environmental factor and estimated the statistical significance of each $\hat{r}$ value. Power was estimated by dividing the number of trials in which both the *true* $\hat{r}$ and the *estimated* $\hat{r}$ (based on recruits generated by VPA) were significantly different from zero and positive by the total number of trials in which the *true* $\hat{r}$ was significantly different from zero and positive. A failure to find a significant $\hat{r}$ with VPA recruitment data constituted a type II error in these cases because $\rho > 0$ and hence, H_0: $\rho = 0$ was false. We estimated mean $\hat{r}$ across trials by first transforming the $\hat{r}$ values for each data set to z values using Fisher's z transform to correct for nonnormality in the distribution of $\hat{r}$ (Zar 1974). The arithmetic mean z value for each 1000 data sets was then transformed back to r to obtain the mean $\hat{r}$ value.

We examined the sensitivity of our results by plotting isopleth diagrams of power using 11 different values for k (or ρ), the true correlation coefficient between recruits and the environmental factor (0.4–0.9 in 0.05 increments), and nine different values for SD_M, the standard deviation of true M (to generate CVs of 0–40% in 5% increments for each of the three hypothetical stocks). As well, a separate isopleth diagram was generated for each of three M^{VPA} values ($\bar{M}$, and the true $\bar{M} \pm 50\%$). The same 1000 sets of random terms for equation 1 were used for each SD_M, k, and M^{VPA} value.

Because the effect of errors in M^{VPA} varies with the relative magnitudes of fishing and natural mortality rates (Sims 1984; Vetter 1988; Bradford and Peterman 1989; Lapointe et al. 1989), we also performed three types of sensitivity analyses: (1) with larger constant F_L values $= \bar{M}$ instead of $0.5\bar{M}$, (2) with variable F_L values (mean $= 0.5\bar{M}$, SD $= 0.25\bar{M}$), and (3) with 10-yr time trends in F_L (minimum $= 0.1\bar{M}$, maximum $= 0.5\bar{M}$). In each case, we gave VPA the true time series of F_L values.

For our baseline simulations, we let SD_N, the true standard deviation of $\log_e$ (recruits) $= 0.3$, a value in the lower part of the range reported for fish stocks (Hennemuth et al. 1980; Myers et al. 1990). In another sensitivity analysis, we examined situations with larger values for SD_N, ranging up to 3.0, the maximum value reported for North Atlantic fish stocks by Myers et al. (1990).

Results

Variability in Estimated Recruits

When the true adult M was constant through time (i.e. $\mathrm{SD}_M = 0$) and $M^{\mathrm{VPA}} = \bar{M}$, the standard deviation (SD) of estimated recruits was equal to the true value (columns 6 and 7 of top row of Table 2). However, when true adult M varied randomly (i.e. $\mathrm{SD}_M > 0$) but VPA estimated recruits by using a constant $M^{\mathrm{VPA}} = \bar{M}$, the SD of estimated recruits was

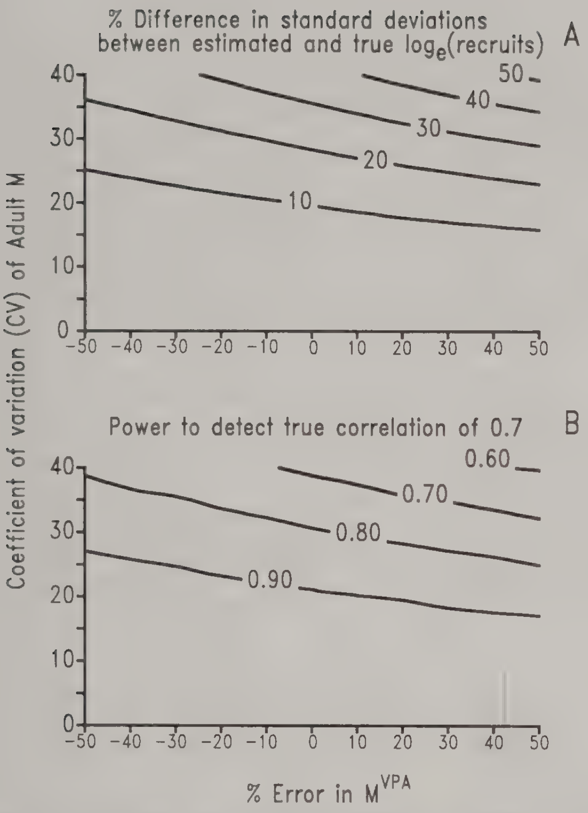

FIG. 1. (A) Isopleths of the percentage difference in standard deviations between the true time series of log$_e$(recruits) and the time series estimated by VPA [100 × (estimated − true)/true] for various coefficients of variation in the true adult natural mortality rate [CV(M)] and different magnitudes of error in the constant natural mortality rate used by VPA (M^{VPA}). (B) Isopleths of statistical power, the probability of correctly detecting a significant correlation between log$_e$(recruitment) and an environmental factor, for the same conditions as shown in Fig. 1A. For both Fig. 1A and 1B, results are for the medium-M stock (Table 1) and for a true correlation between recruitment and the environmental variable (ρ or k) = 0.7.

consistently greater than the SD of true recruitment (columns 6 and 7 of Table 2). Of course, this inflated standard deviation of the time series of estimated recruits reduced the average correlation between true and estimated recruitment below 1.0 to as low as 0.76 for CV in M of 40% (column 5 of Table 2). The difference between the estimated and true SD of recruitment increased as the error in M^{VPA} changed from $\bar{M} - 50\%$ to $\bar{M} + 50\%$ and as variation in adult M increased (Fig. 1A).

Explanation: variability in estimated recruits

Estimated abundance of recruits had larger standard deviations than the true abundance of recruits because the mortality rate used by VPA in each year ($M^{\mathrm{VPA}} = \bar{M}$) will almost always be either greater or less than the true value that year (M_t) and this random error in one of VPA's input parameters increases the SD of estimated abundances. For example, in years when $M^{\mathrm{VPA}} > M_t$, abundance estimates will be larger than the true values, and in years when $M^{\mathrm{VPA}} < M_t$, the reverse is true. These errors propagate back to recruitment abundances because the abundance of recruits is estimated from abundances at older ages as VPA works back in time from the oldest to the youngest fished age (Saila et al. 1985). Thus, the variability in VPA estimates of recruitment consists of two components: (1) random variability resulting from equation 1 (reflected by variable catches-at-age that were given to VPA) and (2) an additional estimation error caused by the use of a constant M^{VPA} rather than the time-varying M_t. For a given CV in M, the percent difference between estimated and true SD increases as M^{VPA} increases from $\bar{M} - 50\%$ to $\bar{M} + 50\%$ (Fig. 1A) for two reasons. First, when $M^{\mathrm{VPA}} = \bar{M} - 50\%$, the number of years when $M^{\mathrm{VPA}} < M_t$ was obviously greater than the number of years when $M^{\mathrm{VPA}} > M_t$. The opposite was true when $M^{\mathrm{VPA}} = \bar{M} + 50\%$. Second, for a given error in M^{VPA}, underestimates of M^{VPA} cause smaller bias in abundance estimates than overestimates of M^{VPA} (Sims 1984; Bradford and Peterman 1989; Lapointe et al. 1989). The combination of a greater frequency of years with M^{VPA} being greater than M_t and the larger bias in those years leads to a larger mean estimation error when $M^{\mathrm{VPA}} = \bar{M} + 50\%$ than when $M^{\mathrm{VPA}} = \bar{M} - 50\%$.

Power to Detect Correlations

The increased variability in estimated recruits (compared with the true recruits) decreased the power to detect correlations between the abundance of true recruits and the environmental variable (last column of Table 2). Power decreased with increases in the CV of adult M and as the error in M^{VPA} changed from $M^{\mathrm{VPA}} = \bar{M} - 50\%$ to $M^{\mathrm{VPA}} = \bar{M} + 50\%$, paralleling the increase in the percent difference in standard deviations of true and estimated recruits (cf. Fig. 1B and 1A).

The mean correlation between the true abundance of recruits and the environmental factor in Fig. 1 was 0.7. When we decreased the ρ value in different model runs (x-axis of Fig. 2), power decreased. For a given ρ value and CV(M), power decreased as $\bar{M}$ increased in our three hypothetical stocks (cf. panels for low-, medium- and high-M stocks in Fig. 2). Power also decreased for each stock as M^{VPA} increased from $M^{\mathrm{VPA}} = \bar{M} - 50\%$ to $M^{\mathrm{VPA}} = \bar{M} + 50\%$ (cf. panels within a given column of Fig. 2).

Figure 2 shows results for simulations in which we assumed $F = 0.5\bar{M}$. Simulations with $F = \bar{M}$ resulted in larger shaded regions (delineating areas where power $\geqslant 0.8$) than shown in Fig. 2. Conversely, a smaller value of F (i.e. $< 0.5\bar{M}$) would have resulted in smaller regions because the effect of errors in M^{VPA} is influenced by the ratio of F_L/M (Vetter 1988; Bradford and Peterman 1989); the smaller the ratio, the larger the effect of errors in M^{VPA}. Simulations with time trends in F_L and variable F_L resulted in the same qualitative patterns as those shown in Fig. 2, but for a given CV(M) and ρ value, power was generally lower, especially for the medium- and high-M stocks.

Simulations with larger variability in true recruitment (SD$_N$) showed that for a given CV(M) and ρ value, power increased with increases in SD$_N$ (Fig. 3A). The effect was most pronounced in the medium- and high-M stocks; low-M stocks showed high power over the entire range of SD$_N$ values (Fig. 3A). To place this effect in perspective, we first determined the threshold SD$_N$ values above which the power was $\geqslant 0.8$ regardless of the CV(M) ($0\% \leqslant$ CV(M) $\leqslant 40\%$) or M^{VPA} value ($\bar{M} - 50\% \leqslant M^{\mathrm{VPA}} \leqslant \bar{M} + 50\%$). Next, we calculated the proportion of stocks in Myers et al.'s (1990) literature survey that had estimates for the SD[log$_e$(recruits)] that were smaller than this threshold (Fig. 3B). For example, with $\rho = 0.7$ and CV(M) = 40%, values of SD$_N \geqslant 0.49$ resulted in power $\geqslant 0.8$ for the medium-M stock. Thirty-two percent of the stocks in Myers et al.'s (1990) survey had estimates for the SD[log$_e$(recruits)] that were <0.49. Similarly, 58% of the stocks had estimates for the SD[log$_e$(recruits)] < 0.77, the

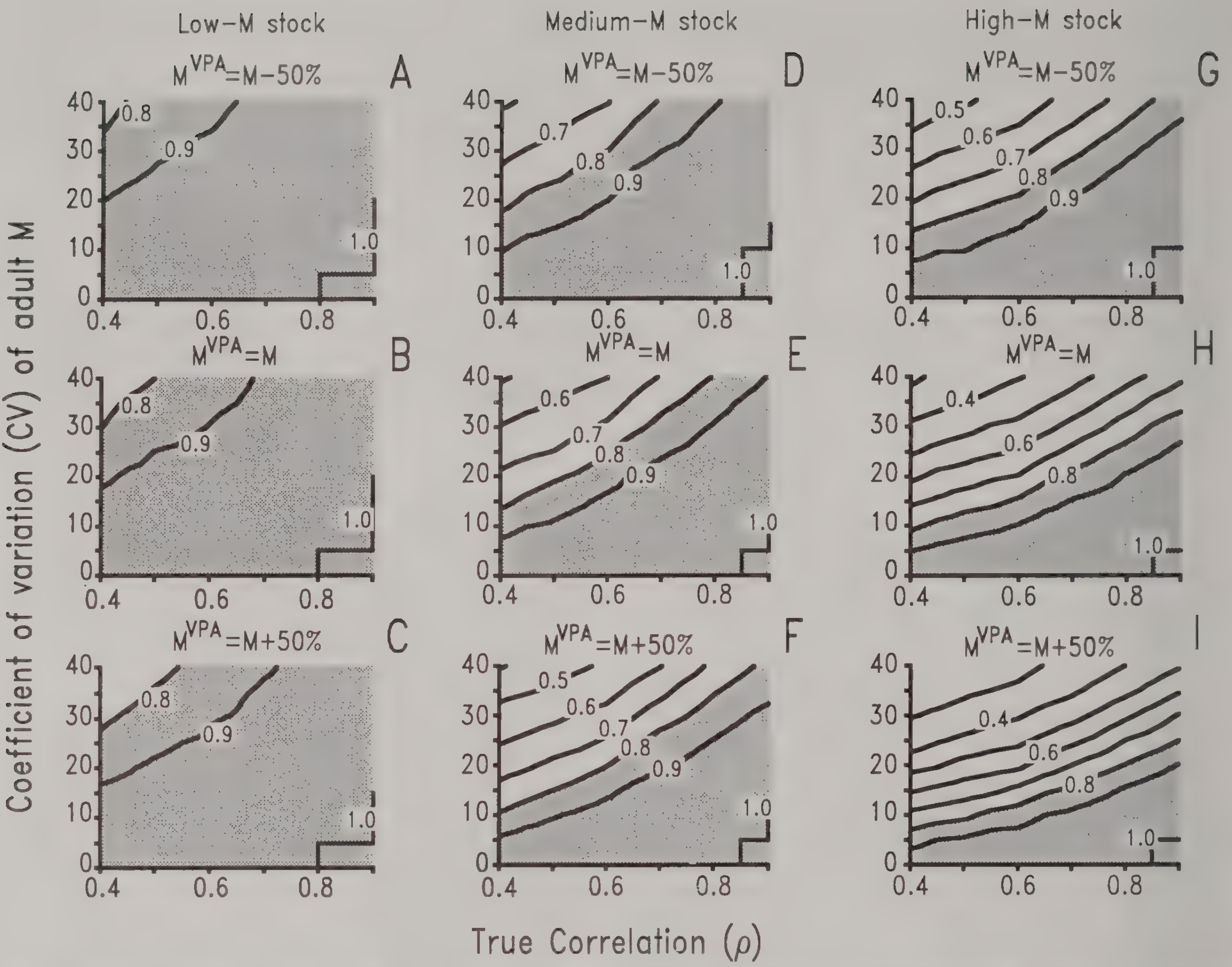

FIG. 2. Isopleths of power to correctly detect a significant correlation between $\log_e$(recruitment) and an environmental factor for various true correlation coefficients (ρ values) for that relationship and various coefficients of variation in the true adult natural mortality rate [CV(M)] [(A–C) low-M stock; (D–F) medium-M stock; (G–I) high-M stock].Shaded areas denote regions where power ≥ 0.8. $M^{\mathrm{VPA}} = \bar{M} - 50\%$ for the top row, $\bar{M}$ for the middle row, and $\bar{M} + 50\%$ for the bottom row. Parameters specific to each stock are given in Table 1 and the fishing mortality rate on the last age class, F_L, was $0.5\bar{M}$ for all three stocks.

threshold value for the high-M stock. Note, however, that 82% of the estimates of SD[$\log_e$(recruits)] given by Myers et al. (1990) were derived from VPA or related methods and therefore are subject to the very bias we document here as well as others noted above. Thus, these numbers can only be used as a rough approximation of the potential number of stocks affected by the bias.

Explanation: power to detect correlations

Power decreased with increased variance in estimated recruits because the increased variance decreased the *estimated* $\hat{r}$ values which decreased the probability of finding a significant correlation (last 2 columns of Table 2). Power increased with increases in the ρ value (Fig. 2) because the power of a test of a correlation increases with increases in the size of the true effect (Cohen 1988). The decrease in power with increases in CV(M) (Fig. 2) follows directly from the patterns in standard deviations described above in the section Variability in Estimated Recruits. Power decreased as $\bar{M}$ increased for a given ρ value and CV(M) because the absolute magnitude of variation in M increased as $\bar{M}$ increased.

Time trends in F_L resulted in lower power for a given CV(M) and ρ value than shown in Fig. 2 because the cumulative fishing mortality rate on cohorts that recruited during the time trend in F_L (i.e. in years 1–9) was lower than for the situation in which F_L was constant at $0.5\bar{M}$, and thus, recruitment estimates for these cohorts were more biased when VPA was given an incorrect M^{VPA} (Lapointe et al. 1989). Randomly varying F_L values resulted in lower power despite the fact that we gave VPA the correct time series of F_L values because VPA estimates F_i values for younger age classes (i.e. for ages $L - 1$ to 1, the age of recruits) in all years except the most recent year and these estimates would have been erroneous by varying amounts depending on the relative values of M^{VPA} and M_t. The errors in F values further exaggerated this variable bias in estimated recruits.

For a given ρ value, power increased with increasing SD_N (Fig. 3A). The explanation for this counterintuitive result requires several steps. First, equations 1 and 2 can generate the same ρ between Y_t and E_t for different values of SD_N. Thus, for a given ρ value, and in the absence of bias (i.e. CV(M) = 0), the estimated SD[$\log_e$(recruits)] equals the true

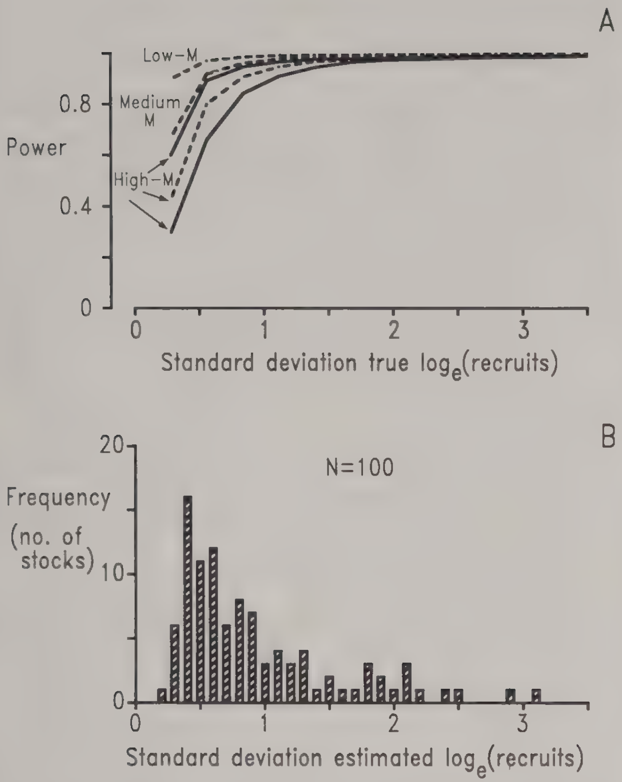

FIG. 3(A). Sensitivity of power to various values of the true SD[$\log_e$(recruits)]. Broken lines denoting results of model runs with $M^{VPA} = \bar{M}$ are shown for the low-, medium-, and high-M stocks. Solid lines, which bracket the broken line for the high-M stock are for $M^{VPA} = \bar{M} - 50\%$ (upper solid line) and $M^{VPA} = \bar{M} + 50\%$ (lower solid line). Solid lines for low- and medium-M stocks (not shown) also bracket their respective broken lines. All results are with a true correlation between recruitment and the environmental variable (ρ or k) = 0.7 and a coefficients of variation in the true adult natural mortality rate [CV(M)] = 40%. (B) Frequency histogram of number of stocks with different estimated SD[$\log_e$(recruits)]. Data from Myers et al. (1990).

SD[$\log_e$(recruits)] (i.e. SD_N) and power will equal 1 regardless of the value of SD_N (e.g. columns 2, 6, 7, and 10 of top row of Table 2). Second, when the true M varies over time but a constant M^{VPA} is used in VPA, estimation error decreases power because it increases the total variation in estimated recruits (columns 7 and 10 of Table 2). Third, the magnitude of the estimation error is independent of the underlying true variation in recruitment. Thus, as the variation in true recruits, SD_N, increases, the estimation error resulting from using a constant M^{VPA} represents a decreasing proportion of the total variation in estimated recruits and power increases.

Discussion

Failure of VPA to account for interannual variability in the true adult natural mortality rate results in recruitment estimates that are more variable than true recruitment. This increased variance decreases the power to detect correlations that might exist in nature between the abundance of recruits and environmental factors. We suspect that random errors in other inputs to VPA (e.g. catches and fishing mortality rates; Rivard 1989) and other biases noted in the introduction may have similar effects. The decreased power was not large under most circumstances investigated here, but the type of bias we document and others noted above have probably contributed to the difficulties researchers have encountered in detecting environmental correlates with recruitment (e.g. Myers and Drinkwater 1989). Thus, just as finding a significant correlation is insufficient evidence for the existence of some causal relationship between the abundance of recruits and an environmental factor (due to potential spurious correlations; Gulland 1953; Lapointe and Peterman 1991), failing to find a significant correlation is also insufficient evidence for the nonexistence of a relationship because the power of such correlation tests may be low (Peterman 1990).

We kept the variation in M constant across ages in the simulations because there are few published examples where the interannual variation in adult M can be estimated. However, if one of the major causes of natural mortality is predation, it is plausible that younger fish may experience higher and more variable M than older fish (e.g. due to M decreasing with increasing size; Peterson and Wroblewski 1984; McGurk 1986). Also, forage species may have more variable M than predator species. Multispecies VPA results support both possibilities (e.g. Daan 1987; Hilden 1988). Age-dependent variation in M might alter our quantitative results but would not affect the qualitative patterns presented here.

We simulated a randomly varying environmental variable rather than a linear or cyclical time trend in order to avoid introducing autocorrelation into the data series. When the environmental variable has a time trend, failing to account for a variable adult M may also decrease power, but interpretations of correlations in such situations are probably more likely to be affected by spurious time trends that can occur in VPA estimates. Lapointe and Peterman (1991) reported that when the environmental factor has a time trend and VPA generates spurious time trends in recruits (due to the mechanism mentioned in the introduction and reviewed in Lapointe et al. 1989), power may be decreased to a greater extent than we have shown here and spurious correlations may even result.

We have documented circumstances under which VPA estimates exaggerate variability in time series of estimated recruitment, but there are other conditions that would have the opposite effect. For example, if M is normally relatively low, and if it increases due to density dependence when abundance is high (particularly for younger ages), Ulltang (1977) suggested that using a constant M^{VPA} would tend to underestimate the strength of strong year classes relative to weak year classes. Unfortunately, lack of good data on variation in M precludes statements here about the frequency and magnitude of this effect. In addition, aging errors cause an underestimation of variation in recruitment because fish from a strong year class are misassigned to age groups in adjacent year classes (Rivard 1989; Bradford 1991). Bradford (1991) found that correlations between recruits (estimated by VPA with aging errors) and a random environmental variable were lower than the true value, but the effect was small unless the aging errors were severe. While Bradford's and Ulltang's biases would tend to counteract the effects of failing to account for variation in M, it is unlikely that they would do so exactly. Thus, the estimated recruitment time series would still not reflect the true temporal variability in recruits.

If analysts had some estimates for the variation in M for particular stocks, our results could be used to at least bound the magnitude of the effect of the bias on estimated variability of recruits and the power to detect correlations. However, in practice, such estimates are rarely available and very difficult to obtain because most methods for estimating M and its variation over time depend on the collection and analysis of representative catch data (see Vetter 1988 for a review of the problems with such analyses). Thus, determining the relative magnitude of the bias for specific cases is a particularly intractable problem.

Fortunately, for stocks like our low- and medium-M stocks, conclusions about the significance of correlations between recruits and environmental factors are reasonably robust to the assumption of a constant annual M^{VPA} over a large range of CV in adult M, possible standard deviations in true $\log_e$(recruits), and true correlation coefficients. Thus, for these stocks, research efforts might best focus on correcting aging error, a more tractable problem than getting unbiased estimates of M.

However, detecting correlations between recruits and environmental factors in high-M stocks will be more difficult if M is variable. Furthermore, the potential counteracting effects of aging error are likely to be the smallest in such stocks, since short-lived stocks are generally less susceptible to aging errors than long-lived stocks (Beamish and McFarlane 1983). This is unfortunate because understanding the causes of recruitment variability in short-lived, high-M stocks may be particularly valuable to management, since incoming recruits usually represent a large proportion of the fishable biomass (e.g. Peruvian anchoveta, California sardine, and northern anchovy).

There are some approaches to dealing with the problem of biased variance in VPA's recruitment estimates for these high-M stocks, but most rely on the availability of additional knowledge about the stock dynamics. First, Hilden (1988) discussed a filtering procedure (Welch 1986) to correct for the assumption of a constant M^{VPA}, but this method appears inadequate because it assumes that the correct functional form of the stock–recruitment relationship is known. Second, like Hilden, we conclude that if independent data are available to identify periods of extreme shifts in M, this may better help to reduce the problem of inflated variance in recruitment estimates. However, in the absence of such independent information, correlation analyses of environmental factors and fish recruitments generated by VPA should include sensitivity analyses. Specifically, a separate time series of recruitments should be generated for each of, say, three plausible M^{VPA} values, each time series correlated with the time series of the environmental variable, and conclusions from each analysis compared. These sensitivity analyses should also include evaluations of the potential for a variable adult M, as discussed above, as well as a trend in F, as discussed by Lapointe and Peterman (1991). Because the absolute magnitude of M^{VPA} and its true variability are unknown for most stocks (Vetter 1988), such analyses cannot be used to estimate the magnitude of either the true variability in recruits or the true correlation between recruitment and an environmental variable, but they can be used to show how robust the conclusions are to various assumed values of M^{VPA}.

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Juvenile Dungeness Crab (*Cancer magister*) Recruitment Variability and Oceanic Transport during the Pelagic Larval Phase[1]

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McConnaughey, R. A., D. A. Armstrong, B. M. Hickey, and D. R. Gunderson. 1992. Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. Can. J. Fish. Aquat. Sci. 49: 2028–2044.

The influence of environmental variability on *Cancer magister* year class strength was examined using trawl survey data from the Washington coast, 1983–88. Average June–September estimates of early instar abundance within two coastal estuaries and the adjacent nearshore are compared with alongshore and cross-shelf transport vectors during the preceding 4- to 5-mo pelagic larval phase. Settlement in the study area varied interannually by nearly 40-fold and was inversely related to net alongshore (northward) transport during January–May. Settlement was confined to a relatively narrow band along the coast and in estuaries; new recruits were rarely encountered beyond 46 m depth, corresponding to a distance of ~15 km from shore. We found no evidence for sustained westward Ekman transport to account for progressive seaward transport of zoeae, as proposed by other authors. Rather, persistent landward transport of near-surface waters will tend to minimize advective loss of larvae to seaward while promoting retention in proximity to suitable juvenile and adult habitat nearshore. Temporal and spatial continuity of northward transport during the winter months, coupled with proximity to high-risk areas downstream, suggests that Washington *C. magister* populations are frequently dependent on larvae originating to the south for recruitment.

L'influence sur les effectifs d'une classe d'âge donnée, chez *Cancer magister* de la variabilité de facteurs écologiques, a été examinée à partir des résultats de recensements obtenus par traits de chalut le long de la côte de l'État de Washington entre 1983 et 1988. On compare la moyenne des estimations, faites entre juin et septembre, de l'abondance des instars, dans leurs premiers stades de développement, à l'intérieur de deux estuaires et en bordure du littoral voisin, avec les dénombrements de sujets dans la phase larvaire pélagique des 4 à 5 mo précédents qui sont transportés le long du littoral et en travers de la plate-forme littorale. La colonisation de la région d'étude variait d'une année à l'autre par un facteur voisin de 40, et elle était inversement proportionnelle au transport net en bordure du littoral (vers le nord) entre janvier et mai. La colonisation se faisait dans une bande assez étroite le long de la côte et dans les estuaires; on trouvait rarement de recrues à plus de 46 m de profondeur, ce qui correspond à une distance d'environ 15 km du rivage. Rien n'indique qu'il y ait un transport Ekman de quelque importance vers l'ouest qui pourrait expliquer le transport progressif vers le large des zoées, comme d'autres chercheurs l'ont proposé. Au contraire, la circulation soutenue vers le rivage de l'eau située à proximité de la surface tend à minimiser les pertes par advection de larves vers la mer en retenant plutôt les larves à proximité d'habitats susceptibles d'être occupés par les juvéniles et les adultes, à proximité de la côte. La continuité dans le temps et dans l'espace (vers le nord) du transport au cours de l'hiver, combinée à la proximité de régions à risque élevé en aval, nous porte à penser que les populations de *C. magister* de l'État de Washington dépendent fréquemment, pour leur recrutement, des larves qui proviennent du sud.

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Meroplanktonic larvae are adapted for long-range dispersal by ocean currents (Thorson 1961; Scheltema 1975), yet are fundamentally responsible for repopulating established areas. A recurring pattern of larval retention, conspicuous among nearshore (Peterson et al. 1979; Bailey 1981; Parrish et al. 1981; Rothlisberg and Miller 1982; Ennis 1986; Roughgarden et al. 1988) and estuarine (Bousfield 1955; Sandifer 1975; Sulkin and Van Heukelem 1982; Epifanio et al. 1989) populations, suggests that significant adaptive value is attached to this strategy. These responses, differentiated primarily by geographical scale, may be attributable to adaptive behaviors which have evolved in response to time-averaged patterns in the circulation. Whereas some species seemingly maximize onshore drift of larvae and depend on coastal transport processes such as internal waves (Shanks 1983, 1986; Jillett and Zeldis 1985) and wind-driven circulation to ensure recruit-

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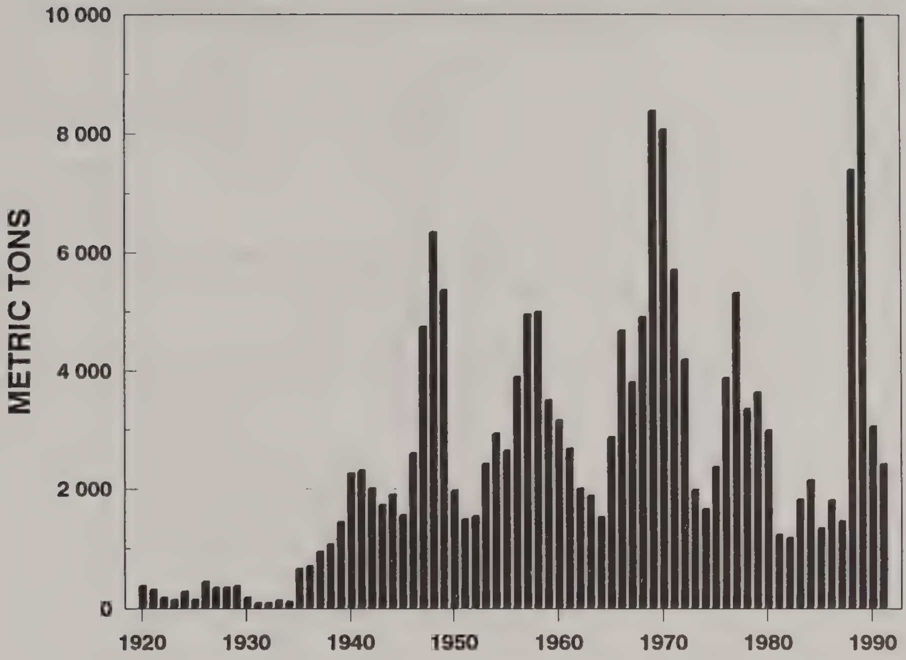

FIG. 1. Coastal Washington Dungeness crab fishery landings, 1920–91.

ment (Peterson et al. 1979; Johnson et al. 1986; Jamieson et al. 1989; Johnson and Hess 1990), others seemingly promote offshore transport, relying, instead, on larger features of oceanic circulation such as countercurrents and coastal gyres (Efford 1970; Phillips 1981; Kelly et al. 1982; Pringle 1986). Given the viscissitudes of environmental forcing, it is reasonable to expect that the abundance of species with a meroplanktonic phase will be responsive to deviations from the long-term mean hydrographic regime (see Wooster 1983).

The Dungeness crab (*Cancer magister*) is widely distributed in the eastern Pacific Ocean (Jensen and Armstrong 1987) and supports an important commercial fishery characterized by highly variable and cyclical landings (Fig. 1). Its complex life history is typical of marine invertebrates with meroplanktonic larvae and a broadcast reproductive strategy. In coastal Washington waters, mating occurs primarily in May–June, eggs are extruded in September–October, and larvae are released during January–mid-March (Cleaver 1949; D. Armstrong and T. Wainwright, School of Fisheries, University of Washington, Seattle, WA, unpubl. data). Larval ontogeny requires approximately 130–150 d (Lough 1976) and consists of five zoeal stages and the megalopa stage (Poole 1966; Reed 1969). Settlement occurs in coastal waters and in estuaries primarily during May–June followed, on occasion, by a second smaller pulse later that same year (Stevens and Armstrong 1984; Gunderson et al. 1990; unpubl. data). The rate of growth is highly variable (Tasto 1983; Botsford 1984; Orensanz and Gallucci 1988), and it is generally held that entry into the fishery occurs 3–4 yr after hatching. Most commercial fishing occurs in coastal waters less than 40 m deep (PMFC 1978). This corresponds closely with the depth limit (~50 m) within which typical wave activity along the Washington coast prevents deposition of silt (Kachel and Smith 1989), suggesting that crab distribution reflects systematic changes in substate characteristics and associated benthic communities (Lie and Kisker 1970).

Previous attempts to explain interannual variability in *C. magister* abundance have been largely unsuccessful (reviewed by Hankin 1985; Botsford et al. 1989). Most attempts have relied on time-lagged relationships between physical features of the environment during the planktonic larval phase and subsequent commercial landings (Peterson 1973; Botsford and Wickham 1975; ; Wild 1980, 1983; Love and Westphal 1981; Johnson et al. 1986). This approach, however, neither accounts for the multiyear class nature of the fishery nor addresses whether year class strength reflects the fate of larvae or benthic juveniles (see Bakun et al. 1982). Recent field studies off Vancouver Island and Washington (Jamieson and Phillips 1988; Jamieson et al. 1989) and the U.S. Pacific coast (Hobbs et al. 1992) suggest that coastal currents may affect the spatial distribution of megalopae and subsequent recruitment levels. Other studies have considered biotic factors and were themselves inconclusive (Botsford and Wickham 1978; McKelvey et al. 1980; Botsford et al. 1983; Thomas 1985). Variation in the spawning stock has generally been dismissed as a contributing factor based on the general absence of a spawner–recruit relationship in Crustacea (Caddy 1986), low interannual variability in female *C. magister* abundance (Hobbs et al. 1992), and a widely held belief in surplus production of eggs and larvae. Moreover, strong *C. magister* year classes typically follow periods of low (spawning) stock abundance (Fig. 1), further reducing the likelihood of a functional spawner–recruit relationship.

In this study, we examine the influence of oceanic larval transport on year class strength measured at the time of settlement to the benthos using trawl survey data collected along the coast of Washington and in adjacent estuaries during 1983–88. We hypothesize that larvae do not reach optimal juvenile habitat nearshore and in estuaries and that strong year classes are not possible, unless the coastal circulation retains larvae nearshore

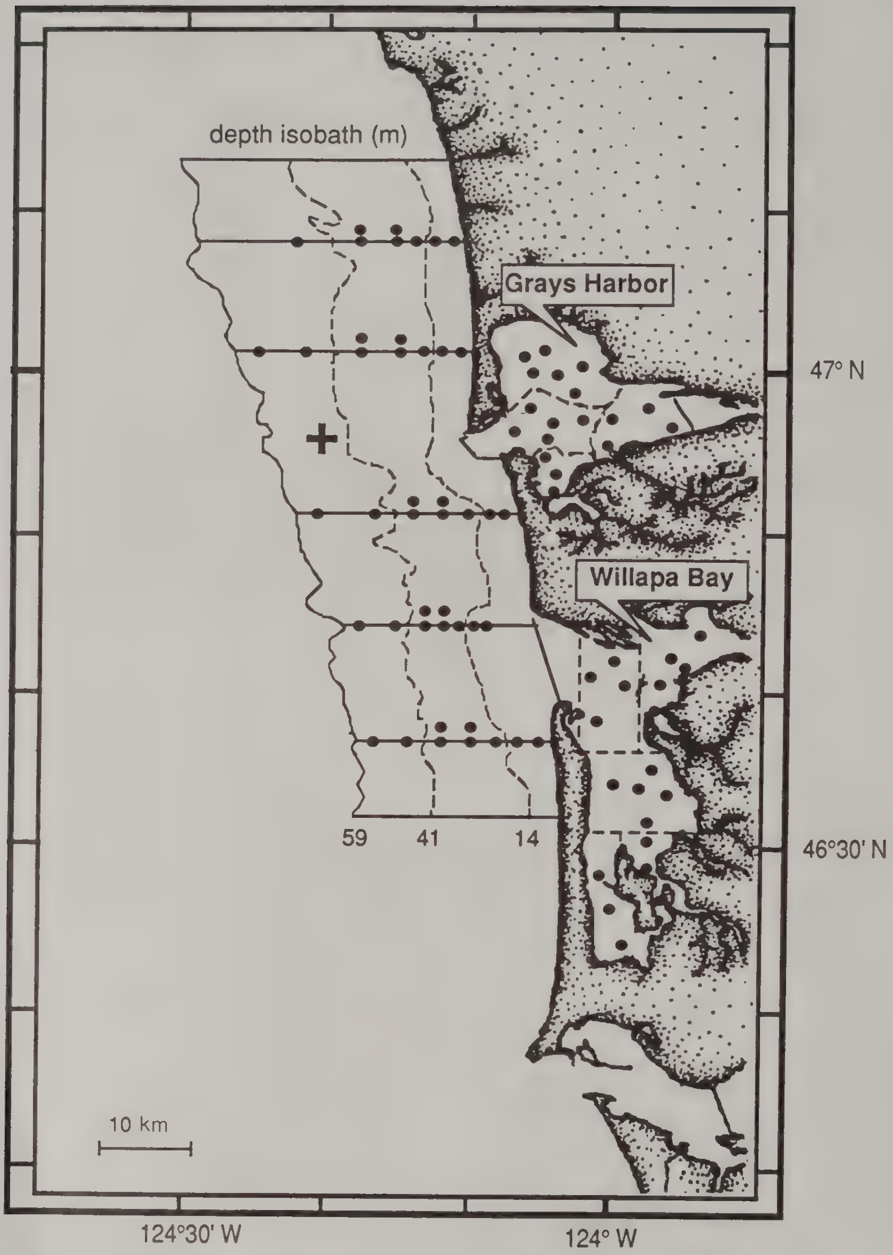

FIG. 2. Study area along the southern Washington coast. Shown are subsystem boundaries, nearshore transect lines, trawl stations (solid circles), and the site (+) selected for Ekman transport data used in the analyses. Broken lines indicate survey stratum boundaries.

and in relative proximity to suitable benthic habitat. Furthermore, we speculate that interannual variation in recruitment to coastal populations is closely linked to alongshore advective processes. Our conclusions diverge from the prevailing recruitment paradigm for the species, which stresses cross-shelf advection of larvae. This divergence may reflect consideration for the first time of alongshore geostrophic flow as a factor affecting *C. magister* dispersal.

Data and Methods

Study Area

The study area is situated along the southern Washington coast and comprises both nearshore and estuarine components (Fig. 2). The nearshore area extends from the shoreline seaward to a depth of 59 m. It encompasses an area of nearly 146 600 ha at mean lower low water. This constitutes approximately 40%

of the suggested range of the southern Washington – northern Oregon crab stock (Barry 1985). Also included are the two major estuaries along the Pacific coast of Washington, namely Grays Harbor (8546 ha) and Willapa Bay (11 199 ha), which have been described as important nursery areas for *C. magister* (Stevens and Armstrong 1984; Armstrong and Gunderson 1985; Gunderson et al. 1990).

Survey Design and Protocol

Generally, surveys were conducted throughout the study area during May–September 1983–88 (Willapa Bay; 1985–88; see Gunderson et al. 1990 for details). The nearshore area was sampled along fixed transects oriented east–west (Fig. 2). Trawl stations were located at discrete depths, ranging from the edge of the surf zone at 6 m to the outer limit of crab abundance at 55 m. Three depth strata grouped the two shallowest (6, 9 m), the three intermediate (18, 27, 36 m), and the two deepest (46, 55 m) stations together. Stratum boundaries followed the mean lower low water and the 14-, 41-, and 59-m isobaths. Sampling in the two estuaries was stratified geographically (Fig. 2). Within each stratum, stations were randomly selected from a 1-km^2 grid, with the constraint that no two stations were immediately adjacent to one another.

Survey samples were collected throughout the study area using a modified 3-m plumb staff beam trawl (Gunderson and Ellis 1986). This system was scaled for use aboard a 6.4-m Boston Whaler within estuaries and for larger commercial fishing vessels (11–21 m) along the open coast. Effective width of the net was 2.3 m, while the estimated vertical opening was 0.6 m. Tows of known distance were taken parallel to isobaths in the nearshore and along the main axis of the waterway in the estuaries. The average distance towed was approximately 750 m in the nearshore and 260 m in the estuaries, with mean towing speeds of 2.6 and 2.8 km·h^{-1}, respectively. Crab present in trawl samples were sexed, counted, and carapace widths measured inside the tenth anterolateral spines.

Crab Settlement

We measured settlement success by the average abundance of 0+ (young-of-the-year) crab in the study area during the June–September period of each year. Average abundance (N_i) was calculated as

$$(1)\quad N_i = \frac{1}{4}\sum_{j=6}^{9} \mathrm{GH}_{ij} + \mathrm{NS}_{ij} + \mathrm{WB}_{ij}$$

where i = year (1983–88), j = month (June–September), GH = 0+ abundance in Grays Harbor, NS = 0+ abundance in the nearshore, and WB = 0+ abundance in Willapa Bay. It is assumed that this index better reflects settlement magnitude than a measure based on a single month, given the patchy distribution of the instars and interannual variability in the timing of settlement (Gunderson et al. 1990). Statistical analysis of the nearshore data indicated that these months constitute a homogeneous group with respect to abundance (Fig. 3). Population estimates for each area were generated using area-swept procedures (Gunderson et al. 1990). The missing Willapa Bay components for 1983 and 1984 were estimated using multiple regression methods ($P < 0.001$, $R^2_{\mathrm{adj}} = 0.86$). The following model was selected on the basis of the adjusted coefficient of determination (R^2_{adj}) and appropriateness of the error structure:

$$(2)\quad \log_e \mathrm{WB} = 0.97 \log_e \mathrm{GH} - 0.34\ \mathrm{MONTH} - 2.91$$

where WB = 0+ abundance in Willapa Bay, GH = 0+ abundance in Grays Harbor, and MONTH = May–September, coded as 5, 6, 7, 8, 9. Predicted values were exponentiated and incorporated into calculations of total 0+ abundance (eq. 1). Population estimates from semimonthly Grays Harbor cruises during 1983 and 1984 were averaged to provide a single value for the month.

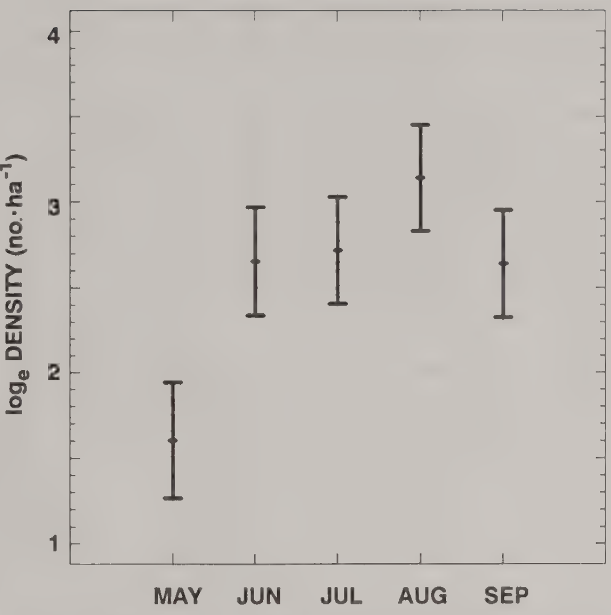

FIG. 3. Monthly means and 90% CIs for $\log_e$-transformed 0+ crab densities in the nearshore area; all years pooled by month. One-way ANOVA ($P < 0.001$) and 90% Tukey test indicate two homogeneous groups of months: (1) May and (2) June, July, August, and September.

The upper carapace width limits for the 0+ age class were determined by inspection of modes in length–frequency plots, a relatively straightforward task for this age class (Fig. 4).

The nearshore data were examined for detectable interannual differences in instar density using ANOVA and Tukey's multiple comparison procedure. Given that the nearshore regularly contributes the majority of 0+ crabs in the study area (Gunderson et al. 1990; this study), significant differences there are likely to reflect the pattern for the full study area. Subsequent discussions of interannual patterns are based on expanded population estimates of 0+ crab in the full study area (eq. 1).

Our hypothesis concerning the existence of optimal juvenile habitat and the requirement that settlement occur close to shore is consistent with observations in the literature (e.g. Carrasco et al. 1985). ANOVA and Tukey's multiple comparison procedure were applied to nearshore catch data pooled according to depth, in order to test this assumption. The selective nature of substrate retention by our trawl precluded a detailed analysis of 0+ densities in various substrates; finer materials such as silt and sand typically were lost from the net prior to examination. However, standard trawls (n = 43), in conjunction with sidescan sonar, box core, and grab-sample assessments of substrate, were conducted in a representative area (depths 18–46 m) seaward of Grays Harbor during June 1985. Substrate was classified on the basis of grain size and percentage distribution of the major fractions (W. Pearson, Batelle Laboratories, Sequim, WA) as either gravel (>2.00 mm), sand (0.063–2.00 mm), or silty sand (sand with >10% silt and clay). These data were used to compare mean 0+ densities in the three types of substrate.

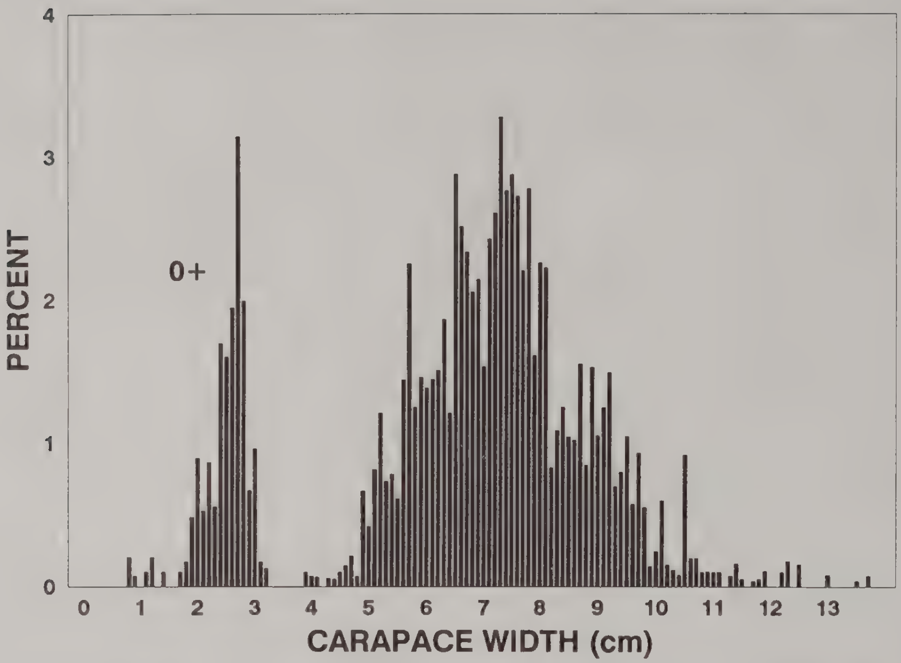

FIG. 4. Representative (July 1985) *C. magister* length–frequency diagram (n = 1178). Note the clear demarcation between 0+ and subsequent age classes.

Physical Forcing

Ekman transport (ET)

ET describes wind-driven circulation as a function of the wind stress (Ekman 1905; Stacey et al. 1986). It is of primary importance to cross-shelf circulation and also contributes to alongshore transport, which is functionally dominated by geostrophic flow. Calculated winds, as well as northward and eastward components of associated ET, were obtained as part of a standard product available from the National Marine Fisheries Service Southwest Fisheries Center (D. Husby, Monterey, CA). Calculated wind vectors and associated ocean transport indices (Bakun 1973) are based on 6-h pressure field values prepared by the U.S. Navy Fleet Numerical Oceanography Center. The ET values obtained represent the depth integrated (''mass'') transport per unit width of ocean surface (MT per second per kilometre) moving at 90° to the right (in the Northern Hemisphere) of the wind vector. We have limited the ET rotation to 45°, given the progressive deflection of wind-driven flow with depth (the familiar ''Ekman spiral'') and the reported near-surface orientation of *C. magister* zoeae and megalopae (Lough 1976; Jacoby 1982; Reilly 1983; Jamieson and Phillips 1988; Jamieson et al. 1989). This angle represents a time-averaged value for vertically migrating zoeae and megalopae that spend equal periods of time in neustonic waters (moving at low angles to the wind; Stacey et al. 1986) and at depth moving normal to the wind (cf. Hobbs et al. 1992). The 6-h ET records are resolved into northward and eastward components. These data form an attractive set for analysis because they are temporally complete and derived by a common process and, as such, are used extensively in this and other fisheries applications as indicators of wind-driven currents.

In order to compensate for frictional effects, Bakun's (1973) estimate of surface winds incorporates a simple correction whereby calculated wind speed is reduced by 30% and wind vectors rotated 15° counterclockwise. However, Halliwell and Allen (1984, 1987) demonstrated a misalignment between calculated and *measured* winds along the west coast of North America and concluded that Bakun's rotational correction (15°) is insufficient for coastal areas (see also Hsueh and Romea 1983; Thomson 1983). Wind veering due to coastal topography, surface horizontal temperature gradients, and diurnal winds requires an additional rotational correction for calculated winds at or near the coast. This correction varies as a function of position along the coast: ranging between 5 and 50° counterclockwise over alongshore distances of a few hundred kilometres (Halliwell and Allen 1987). For most locations, seasonal differences are small and a single annual correction is appropriate. However, winter cross-shelf winds are more energetic than alongshore winds at Grays Harbor, probably due to the relatively low coastal mountain barrier found there. Hence, seasonal corrections are required for this area. Corrections which have been applied while computing corrected Ekman transport vectors (ET′) are summarized in Fig. 5.

A position central to the study area (46°55′N, 124°20′W; Fig. 2) was selected and daily means of ET′ were computed. Large coherence scales (>500 km alongshore and ~200 km cross-shelf; Hickey 1989) suggest that calculations for a fixed position adequately reflect conditions experienced by larvae during transport away from this point. Transport distances were derived from calculated ET′ volumes using standard formulas and a representative eddy viscosity coefficient (100 $g \cdot cm^{-1} \cdot s^{-1}$, with a corresponding Ekman depth of 43 m; Neumann and Pierson 1966); estimation was relatively robust with respect to the parameters. For example, a 20% increase/decrease in the eddy viscosity coefficient caused an approximate 5–12% change in (northward and eastward) ET′ distance.

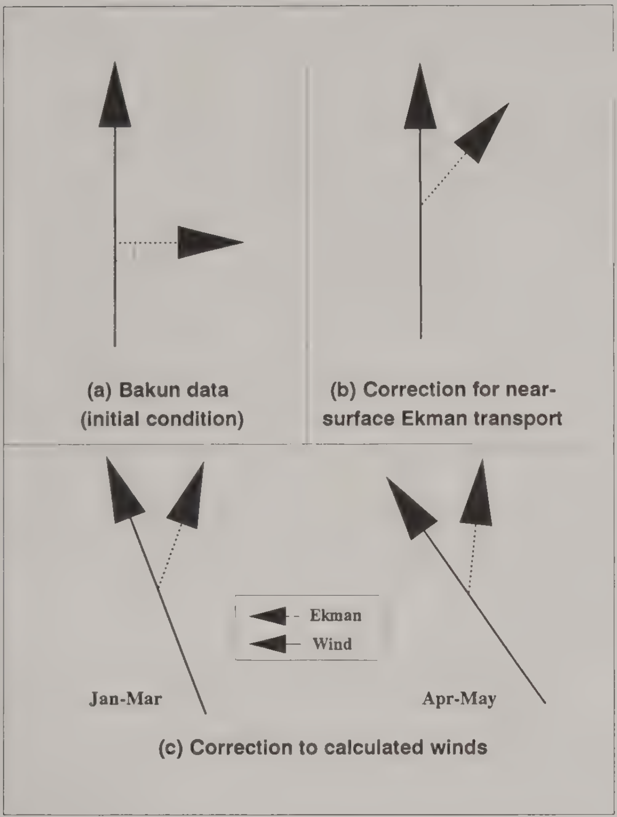
(a) Bakun data
(initial condition)
(b) Correction for near-surface Ekman transport
Ekman
Wind
Jan-Mar
Apr-May
(c) Correction to calculated winds

FIG. 5. Rotational corrections applied to (a) the original (Bakun) Ekman transport vectors for the study area. These vectors were corrected to account for (b) the near-surface orientation of *C. magister* larvae (Ekman rotation limited to 45° clockwise) and (c) the misalignment between calculated and measured winds in coastal areas (original wind and associated Ekman transport vectors rotated 26° counterclockwise during January–March and 39° counterclockwise during April–May for our study area). Net rotational correction applied to Ekman transport vectors (i.e. b + c) is 71° (winter) or 84° (spring) counterclockwise.

Geostrophic transport (GT)

In the Pacific Northwest, alongshore wind stress can drive a relative (geostrophic) current that flows in the direction of the wind and, as such, represents the balance between pressure gradient forces associated with sea level slope and the Coriolis force. During winter, a large buildup of water along the coast due to strong northward winds (and landward ET) results in a correspondingly strong northward geostrophic current as water moving downslope (seaward) is redirected by the Coriolis force. During spring, relatively moderate southward winds (and seaward ET) deplete water along the coast and drive a southward geostrophic current. Mean alongshore geostrophic current velocities over the continental shelf were estimated from adjusted sea level according to

$$(3)\quad fv = g\,\Delta h\,\Delta x^{-1}$$

where f = Coriolis parameter ($7.29 \times 10^{-5}\cdot\mathrm{s}^{-1}$), v = alongshore current velocity (centimetres per second), g = gravitational acceleration (9.8×10^2 $\mathrm{cm}\cdot\mathrm{s}^{-2}$), Δh = adjusted sea level (centimetres), and Δx = shelf width (5.78×10^6 cm). Equation 3 assumes that alongshore geostrophic currents are essentially depth independent and that sea level slope is constant across the shelf; sea level is assumed to be zero at the shelf edge and a maximum at the coast (cf. Huyer et al. 1978). Hourly "staff-zero" tide heights for a position near the mouth of Willapa Bay (Fig. 2; NOS station No. 9440910, Toke Point, WA; S. Lyles, NOAA/National Ocean Services Tidal Datum Section, Rockville, MD) and atmospheric pressure fields provided with the calculated wind data were used to compute the adjusted sea levels. Short data gaps ($\leq$12 h) in the atmospheric pressure time series were filled using linear interpolation, while larger gaps in the tide height and pressure series were bridged using maximum entropy spectral analysis (Andersen 1974). Diurnal and semidiurnal tides were removed from the (suitably extended) tide height time series using Godin's (1972) low pass filter. Adjusted sea levels were calculated by adding deviations in atmospheric pressure from the 1000-mb standard pressure to tide heights averaged over 6 h (to obtain total subsurface pressure) and, finally, by demeaning with the long-term pressure-corrected height:

$$(4)\quad \mathrm{ASL} = [\mathrm{HT} + (\mathrm{AP} - 1000)] - H_p$$

where ASL = adjusted sea level (centimetres), HT = detided staff-zero height (centimetres), AP = atmospheric pressure (millibars), and H_p = long-term mean AP-corrected HT (centimetres). Average daily GT distances were calculated using 6-h current velocities (eq. 3) for the 1983–88 larval periods. Because of the demeaning process, the adjusted sea levels are relative to the long-term mean and corresponding GT distances should be considered as minima. Staff-zero heights were unavailable for 1–12 January 1986 due to a malfunctioning tide gauge and, since the interval was too long to bridge reliably, the GT distances for the period 13–24 January were substituted.

Results

Crab Settlement

The magnitude of crab settlement within the study area varied considerably over the 6-yr period, and three homogeneous groups of survey years were identified statistically on the basis of nearshore settlement densities (Fig. 6). Heavy settlement occurred during 1984 and 1985 with overall (arithmetic) mean 0+ crab densities of 2472 and $4654\cdot\mathrm{ha}^{-1}$, respectively, for the June–September interval. (This ranking for 1984 and 1985 using the arithmetic mean is the reverse of that indicated in the $\log_e$-scale of Fig. 6; this reflects a few extremely large catches taken in the nearshore during July 1985 and their disproportionate effect on the arithmetic estimate; see McConnaughey and Conquest 1993 for a detailed discussion of this issue.) Moderately strong settlement during 1983, 1987, and 1988 was reflected in intermediate mean densities (185, 916, and $574\cdot\mathrm{ha}^{-1}$, respectively). A substantially lower mean density ($55\cdot\mathrm{ha}^{-1}$) was observed during 1986. During most years, only a nominal portion of the total 0+ settlement occurred subtidally in the estuaries (Fig. 7). Although subtidal densities in the estuaries are routinely high (Fig. 8), the surface area is small relative to the nearshore, hence the dominance of the nearshore as regards overall abundance. During 1984 and 1985, expanded population estimates for the full study area were high, with a monthly (June–September) average of 292 million 0+ crab in 1984 and 501 million during 1985 (Fig. 7). Monthly 0+ abundance averaged 31 million during 1983, 131 million during 1987, and 75 million during 1988. The estimate of 13 million 0+ crab for 1986 reflected the lowest recorded settlement during the 6-yr study period.

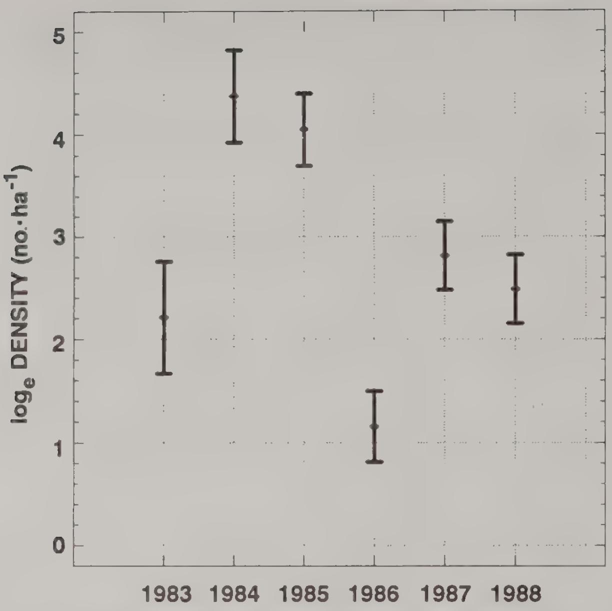

FIG. 6. Annual means and 90% CIs for $\log_e$-transformed 0+ crab densities in the nearshore area; months June–September pooled by year. One-way ANOVA ($P < 0.001$) and 90% Tukey test indicate three homogeneous groups of years: (1) 1986, (2) 1983, 1987, and 1988, and (3) 1984 and 1985.

The distribution of early crab instars varied considerably according to depth, with a trend toward lower densities at increasing distance from shore (Fig. 8). Mean 0+ crab density was comparable at depths ranging from 5 to 37 m, declined significantly at 46 m and again at a depth of 55 m. Limited sampling at 64 m during 1983 and 1984 (n = 14 standard trawls) failed to catch a single 0+ crab (unpubl. data). Similarly, 0+ crab were present in trawls (n = 20) taken from NOAA's R/V *Miller Freeman* during November–December 1983 at depths ranging from 22 to 48 m and were absent thereafter to over 104 m (unpubl. data). Relatively high settlement also occurred in the estuaries, as indicated by a summary measure of density for Grays Harbor and Willapa Bay combined ("E", Fig. 8). This is in keeping with the prevailing cross-shelf pattern of increasing density toward shore and is indicative of the open nature of the nearshore–estuarine complex.

The density of 0+ crab in the nearshore varied considerably according to substrate composition (Table 1). Generally, crab density decreased as substrate coarseness increased. The mean density in silty sand (36 370·ha^{-1}) exceeded that in ordinary sand (3856·ha^{-1}) which itself exceeded the mean density found in gravel (99·ha^{-1}). Statistical comparison of means by ANOVA was inconclusive (P = 0.28), probably because of small sample sizes and the correspondingly low precision of the point estimates. Examination of length–frequency data for the 0+ crab in sand and gravel indicated that a combination of first, second, and third instars was represented on the sand substrate but that second and third instars were notably absent from gravel (Fig. 9).

Physical Forcing

Ekman transport (ET)

Progressive vector diagrams (i.e. daily mean vectors aligned end-to-end, Fig. 10) present a graphical summary of ET′ during the January–May larval period of each year, while net alongshore and cross-shelf transport distances are detailed on a monthly basis in Table 2. The near absence of sustained westward (seaward) transport was particularly notable during the years studied. Net cross-shelf transport was landward in 29 of the 30 months examined. Reversals to seaward transport, although fairly common, were rapidly offset by subsequent landward transport. For example, the large seaward "bulge"

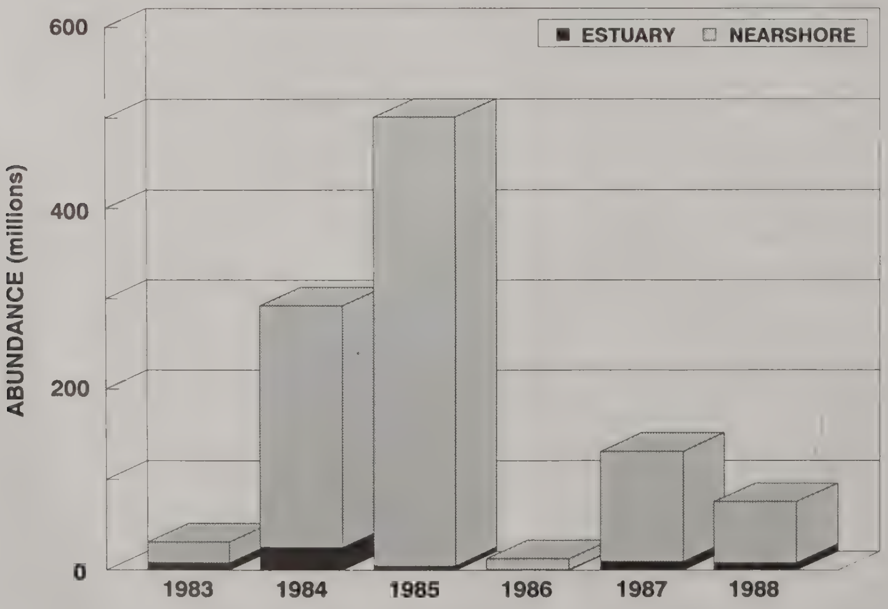

FIG. 7. June–September estimates of average 0+ crab abundance for the full study area, 1983–88. Shown are the relative proportions of subtidal recruits in the nearshore and the estuaries combined.

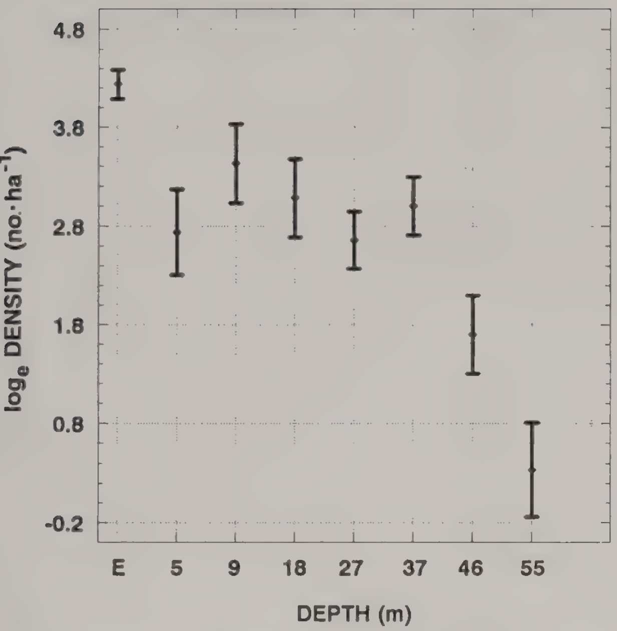

FIG. 8. Pooled means and 90% CIs for log$_e$-transformed 0+ crab densities in the nearshore according to depth. One-way ANOVA ($P < 0.001$) and 90% Tukey test indicate three homogeneous depth groups: (1) 5, 9, 18, 27, and 37 m, (2) 46 m, and (3) 55 m. "E" signifies summary measure for Grays Harbor and Willapa Bay estuaries combined.

TABLE 1. Young-of-the-year (0+) crab density according to substrate composition for coordinated sidescan sonar-trawl survey in the coastal settlement zone near Grays Harbor, June 1985.

Substrate type	Sample size	Mean density (no.·ha^{-1})	SE
Silty sand	27	36 370	21 598.9
Sand	10	3 857	1 642.2
Gravel	6	314	98.7

in the 1984 plot formed over a period of 9 d and persisted only 4 d thereafter (Fig. 10). More extensive seaward transport occurred during January 1985 (31 d) and 1988 (8 d). However, only during 1985 was a net seaward displacement (41 km) recorded for a month. Brief "rotary" patterns were apparent during most years. In all cases, a net landward position was established by February and maintained thereafter.

Overall, alongshore ET′ was much more variable than was the landward component (sample ranges 623 and 185 km, respectively) and had an obvious seasonal pattern (Fig. 10; Table 2). Net alongshore ET′ during January–March ("winter") was consistently northward and was generally southward during April–May ("spring"), with notable exceptions during 1984 and 1988. During 1984, net alongshore ET′ continued northward during April and was only marginally southward during May, while in 1988, it was oriented northward during all months (Table 2). Extensive northward ET′ was apparent during 1983 (783 km), 1986 (899 km), and 1987 (698 km). Northward ET′ was exceptionally strong during January 1986 (averaging 20 km·d^{-1}). In contrast, reduced northward ET′ occurred during 1984 (582 km), 1985 (276 km), and 1988 (452 km). January–May 1985 was remarkable as a period of relatively weak northward (and landward) ET′ along the Washington coast.

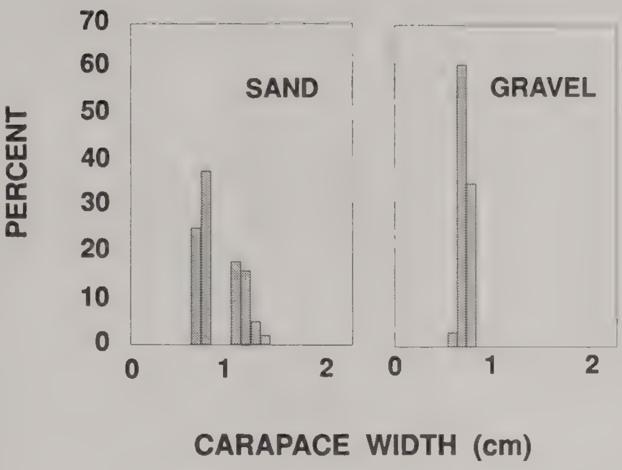

FIG. 9. Length–frequencies of 0+ crab in sand and gravel substrates during the June 1985 coordinated sidescan sonar-trawl survey. Note multiple instars present in sand (mean size ~9 mm) as compared with first instar only (mean size ~7 mm) in gravel.

Geostrophic transport (GT)

Strong northward transport, interspersed with brief periods of relaxation, characterized the winter months of each year, while the spring months were distinguished, to varying degrees, by southward mean flow (Fig. 11). This pattern is consistent with seasonal mean circulation described for shelf waters off Washington (Hickey 1989; and others). Overall, GT was highly variable during the six years examined. Combined northward transport (CNT = GT+ET′, of which GT is the dominant component; Fig. 12) during the pelagic larval phase was extremely strong (5050 km) during 1983, an El Niño year (see Wooster and Fluharty 1985). CNT was also strongly northward during 1986 (3052 km), somewhat weaker during 1984 (2372 km) and 1987 (2485 km), and substantially weaker during 1988 (1450 km). Net alongshore transport during 1985 was southward (CNT = −155 km) for the January–May larval period. Although both GT and ET′ respond to wind forcing, the net GT component for the 1985 larval period was weakly southward, while that for ET′ was weakly northward. This curiosity may reflect early reversal of GT to southward as a result of remote forcing (see Discussion). Broken down by month, a major fraction of CNT prior to the spring transition to southward flow occurred in January and ranged from 28% (1984) to 74% (1988), with an overall mean of 48% (see Fig. 12).

Discussion

Fluctuations in abundance are common among species with meroplanktonic larvae. This has lead to speculation that larval stages are the critical period in the life history of both marine fish (Hjort 1914; Bakun et al. 1982) and marine invertebrates (Thorson 1950, 1966), including *C. magister* (Lough 1976; McKelvey et al. 1980; and others). Large losses during this period are commonly attributed to predation, starvation, and dispersal to unfavorable habitats. The planktonic nature of *C. magister* larvae, coupled with highly variable commercial fishery landings (Fig. 1), has prompted numerous investiga-

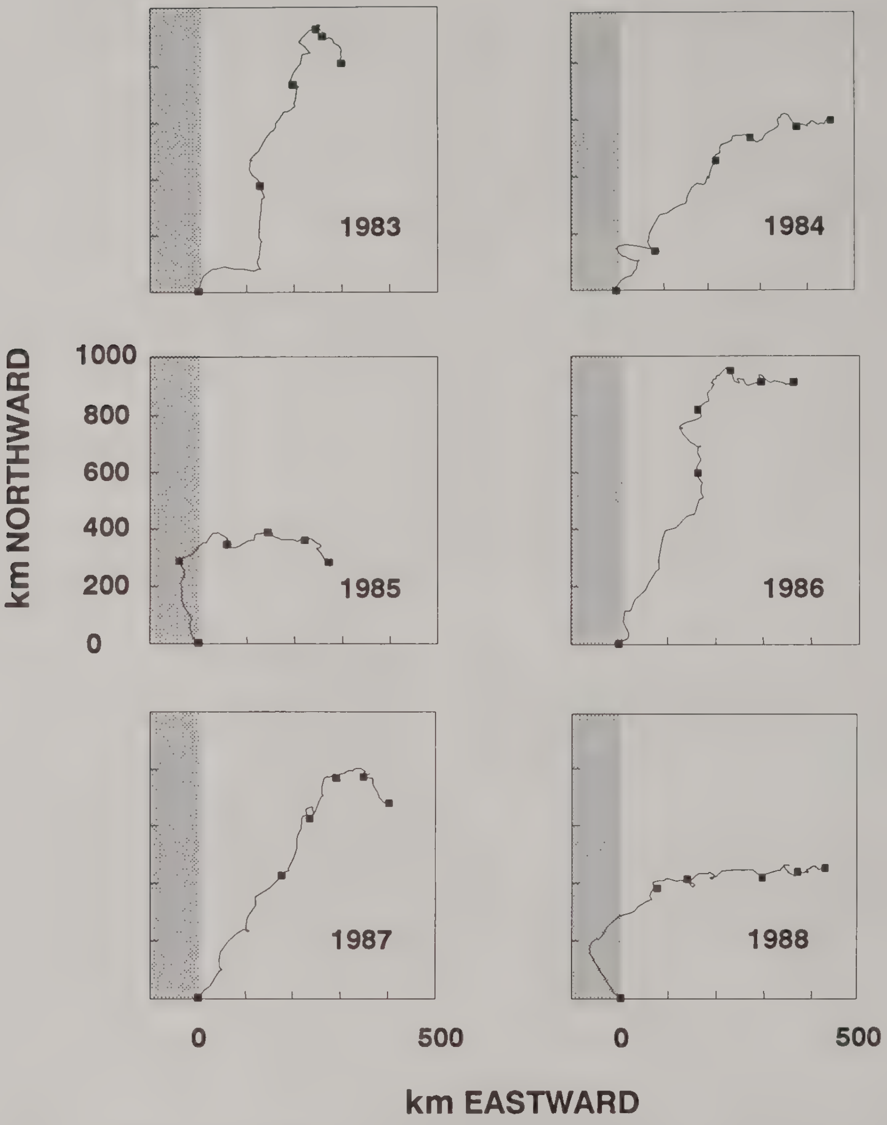

FIG. 10. Progressive vector diagrams of corrected Ekman transport for the January–May larval periods, 1983–88. Northward transport is indicated by a trajectory moving toward the top of the figure, eastward (landward) transport is directed 90° to the right of north, etc. Solid squares designate 30-d intervals, while the shaded box represents net seaward (westward) transport.

TABLE 2. Monthly cross-shelf and alongshore Ekman transport (km) of near-surface waters during January–May of each year. For a position central to the study area, positive (negative) cross-shelf transport corresponds to landward (seaward) direction, while positive (negative) alongshore transport corresponds to northward (southward) direction.

	Cross-shelf						Alongshore					
Year	Jan.	Feb.	Mar.	Apr.	May	Total	Jan.	Feb.	Mar.	Apr.	May	Total
1983	128	76	40	14	51	309	382	345	199	−25	−117	783
1984	78	129	71	99	83	460	142	316	79	45	−1	582
1985	−41	100	85	77	53	275	281	74	28	−28	−80	276
1986	162	9	61	64	65	360	616	200	137	−40	−15	899
1987	184	47	59	58	70	418	438	187	144	3	−74	698
1988	74	65	158	80	58	435	382	32	5	19	14	452

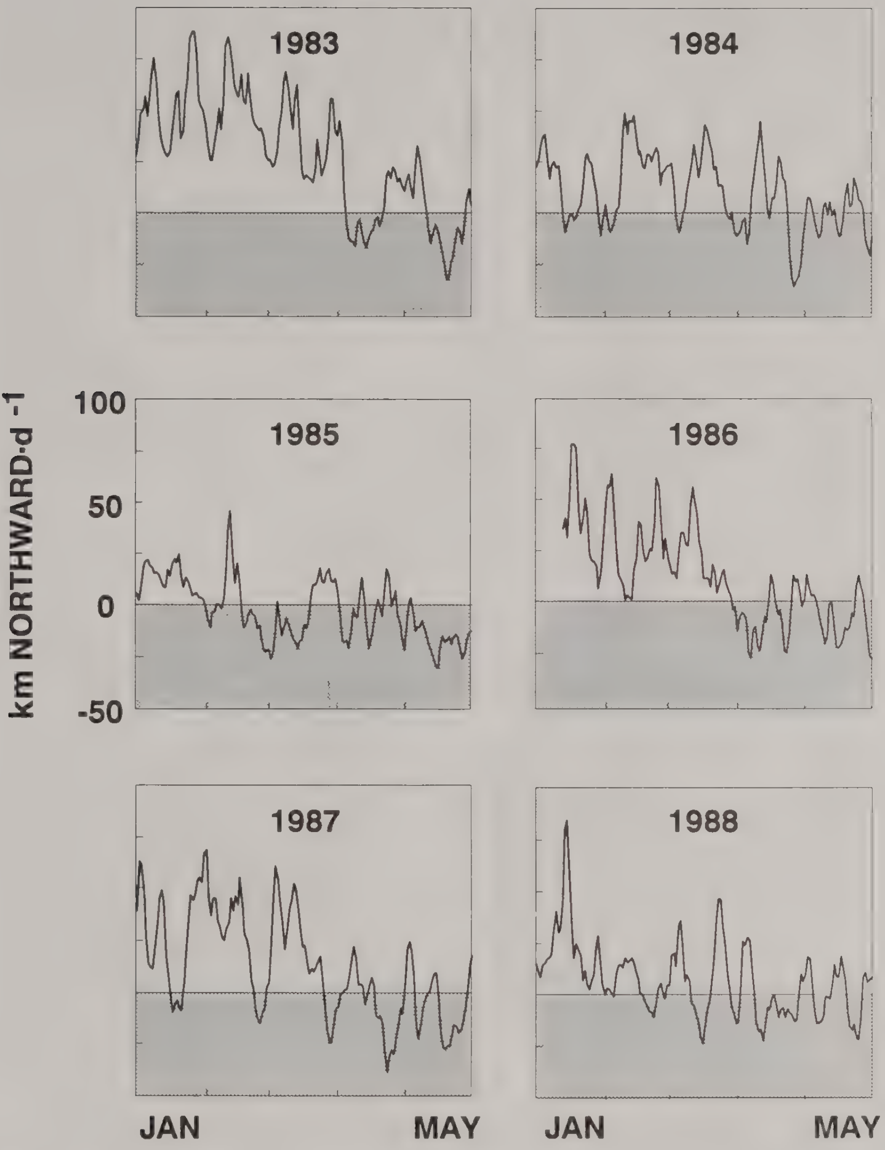

FIG. 11. Daily mean geostrophic transport along the Washington continental shelf near Grays Harbor during the 1983–88 larval periods. Shaded area represents southward transport.

tions into the relationship between transport phenomena and ensuing year class strength. These attempts have been largely unsuccessful due, at least in part, to the lack of abundance measures during larval development and at time of settlement. For the first time, this relationship can be examined directly.

Coastal Settlement Zones

Cancer magister is limited in distribution to a relatively narrow band along the west coast of North America. Most commercial fishing occurs in nearshore waters with silty sand to sand bottoms less than 40 m deep (PMFC 1978), and our surveys indicate that a similar limit exists beyond which successful settlement of megalopae is unlikely (Fig. 8). Even during years of strong settlement, we rarely encountered new recruits beyond 46 m, corresponding to a distance of approximately 15 km from shore near Grays Harbor (Fig. 2). Very little information is available to propose a mechanism reponsible for low crab abundance in fine-grained substrates which are common outside the coastal settlement zone along the Washington coast (depths ⩾50 m; Kachel and Smith 1989; Fig. 13); respiratory complications from sediment accumulation on branchial surfaces (Hochheimer 1988) and inordinately high predation due to lack of protective cover are two possibilities. (It is noteworthy that, contrary to outward appearances, intertidal estuarine sediments where crab are commonly found are, in fact, mostly sand rather than silt and clay.) Within the coastal settlement zone, the coordinated sidescan sonar-trawl survey demonstrated that most recently settled 0+ crab were on sand and silty sand substrate, not on coarser material such as gravel (Table 1). This pattern may reflect behavioral preference for sand by settling *C. magister* megalopae (McMillan 1991). Moreover, relatively rapid declines in abundance on gravel are suggested by the absence of 0+ crab beyond the first instar (Fig. 9). Coarse

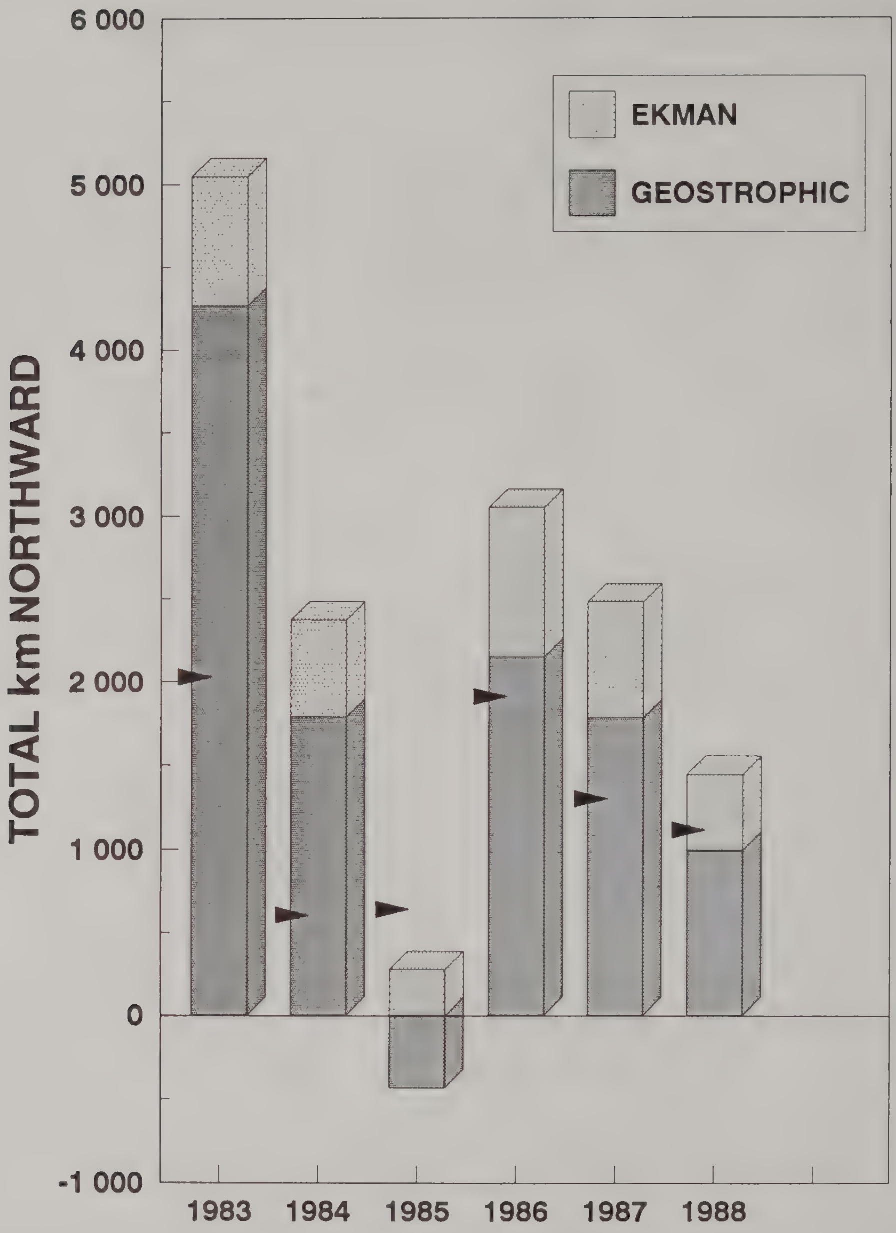

FIG. 12. Combined northward transport (CNT) for continental shelf waters near Grays Harbor during the January–May pelagic larval phase, 1983–88. Arrowheads indicate CNT for the month of January which, in the case of 1985, exceeded total CNT for the period because of subsequently strong southward transport.

substrates not only prevent burial to minimize predation (Schmitt 1921; Dinnel et al. 1986) but are relatively devoid of infaunal and epifaunal species that constitute the juvenile diet (Gotshall 1977; Stevens and Armstrong 1984). Combined, these observations suggest that coarse substrate such as gravel and rock and very fine material such as silt and clay are inferior to open sand as habitat for early *C. magister* instars. Hence, it appears that *C. magister* recruitment may be unsuccessful by virtue of failure to settle within 15 km of the shoreline and, having accomplished that, due to failure to encounter suitable substrate thereabouts.

Progressive Seaward Transport (PST) Hypothesis

Our analyses of coastal transport suggest that a reevaluation of the prevailing conceptual model of *C. magister* larval dynamics may be necessary. Based on field sampling off central California, Reilly (1983) hypothesized PST of larvae through

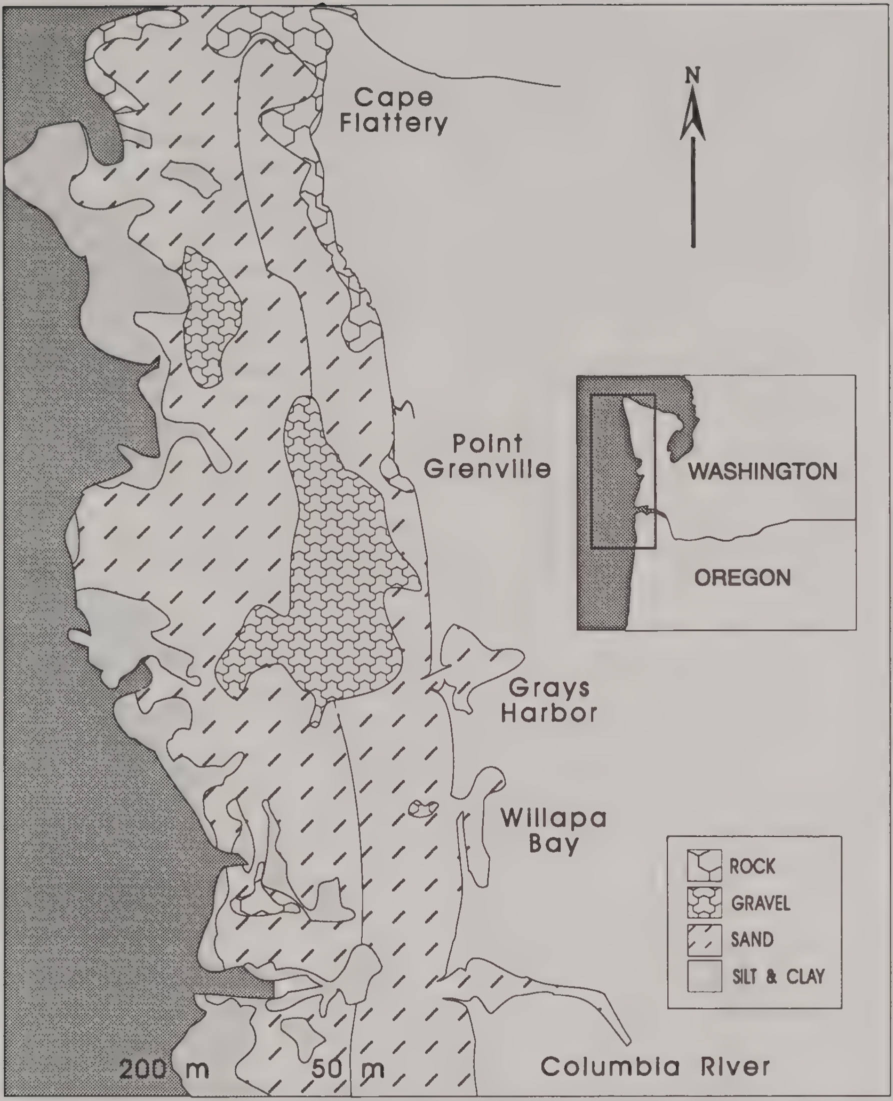

FIG. 13. Distribution of benthic substrate along the Washington continental shelf. Note that coarse material (rock, gravel) is increasingly prevalent along the northern coast. Mean particle size within the sand fraction (0.063–2.0 mm) generally decreases in a seaward direction. (Adapted from 1986 NOAA/National Ocean Service bathymetric fishing maps for the Washington coast).

ontogeny followed by cross-shelf return of megalopae in the spring (Hatfield 1983); alongshore displacement was not addressed. The unspecified mechanism for PST is admittedly problematic given that the inferred direction of larval transport is opposed to the dominant cross-shelf circulation during winter (Hickey 1979; Strub et al. 1987; Fig. 10) and is contrary to the circuit (landward and then seaward) described for *Pandalus jordani* larvae in Oregon waters during the same period (Rothlisberg and Miller 1982; Rothlisberg 1988). An alternative explanation of Reilly's data, based entirely on alongshore transport, is tenable, namely, that early stage larvae were advected northward out of the study area soon after hatching and subsequently returned as megalopae via southward flow. Johnson et al. (1986) postulated such a mechanism, relying on direct downwind transport of megalopae in the neuston. However, Fig. 12 suggests that geostrophic flow, which was not addressed in their study, was probably the dominant mechanism responsible for the presumed southward advection of larvae. There is no evidence in the ET′ series (Fig. 10; Table 2) of sustained seaward transport sufficient to account for large numbers of late-stage zoeae (age 2–3 mo) presumed to be well offshore. In fact, persistent landward drift of surface waters throughout the pelagic larval phase suggests that retention of larvae nearshore is more likely. Lough (1976), similar to Reilly (1983), found early larval stages close to the coast and some later stages further offshore, but concluded that most *C. magister* larvae are retained nearshore by strong alongshore and onshore components of surface circulation. The assumptions concerning the cross-shelf movement of megalopae are less tenuous. Surface waters clearly may move landward during the period that megalopae are present in the water column (Fig. 10; Table 2). Furthermore, intermolt staging of megalopae presents rather compelling evidence for landward transport of this stage, and it has been implied that outer shelf waters (and beyond) constitute the primary source of new recruits for coastal populations (Hatfield 1983; Jamieson et al. 1989; Hobbs et al. 1992). However, the origin (and relative contribution) of these megalopae is unknown and, as such, these studies at best provide only circumstantial evidence in support of the PST hypothesis.

The PST hypothesis may simply be an artifact of very limited nearshore sampling effort and the correspondingly low numbers of late-stage larvae taken. For example, Reilly (1983) failed to catch stage V zoeae during four of the seven years studied, while Lough (1976) found virtually no late-stage larvae. Other studies have been restricted to international waters beyond 3 nautical miles (Jamieson et al. 1989; Hobbs et al. 1992), while the CalCOFI data set described by Reilly (1983) was based on sampling which was concentrated offshore to over 1000 km. In our view, those studies that measure presence (albeit slight) of *C. magister* larvae substantial distances from shore are encountering a small and superfluous proportion of the population. A pronounced shortcoming in the literature on this species is systematic data collected inside 50 m depth during the larval phase where, we believe, most larvae are distributed in years of successful settlement.

Alongshore Transport and Coastal Crab Recruitment

Our analyses suggest that coastal Washington crab recruitment is strongly influenced by interannual variability in alongshore transport. CNT and crab settlement magnitude varied substantially over the years studied (coefficient of variation, (CV) = 73 and 135%, respectively), while cross-shelf transport was relatively constant (CV = 20%). Overall, settlement was inversely related to the extent of CNT during the pelagic larval phase (cf. crab settlement magnitude with CNT in Fig. 14). Settlement was heaviest during years with the least CNT (1984, 1985), while the weakest settlement occurred when CNT was substantially stronger (1983, 1986). Although not statistically different from 1983 (Fig. 6), intermediate-strength settlement during 1987 was associated with an intermediate level of CNT. The 1988 recruitment index was anomalously low (Fig. 7), considering an ET profile (strongly landward; Fig. 10) and CNT regime consistent with strong settlement. Conceivably, high mortality soon after settlement to the benthos (cf. Armstrong and Gunderson 1991; McConnaughey 1991) or an extremely patchy settlement pattern may have caused strong settlement to go undetected by the surveys. In addition, poor recruitment may have been related to the extreme storm event which occurred during 14–16 January of that year (Fig. 11; CNT ≈ 275 km) and the high percentage of the total CNT that occurred during that month (Fig. 12).

As larvae are advected northward along the Washington coast, the likelihood for successful recruitment declines due to unfavorable winds and a preponderance of suboptimal habitat. Mean wind vectors, and hence, wind-driven transport, rotate progressively seaward north of Grays Harbor (Thomson 1981; Halliwell and Allen 1987; also see Strickland and Chasan 1989), increasing risk of transport away from suitable habitat close to shore. Even when larvae are retained in relative proximity to the coastline, the risk of encountering coarse (and thus less adaptive; Table 1, Fig. 9) substrate increases dramatically along the northern Washington coast (Strickland and Chasan 1989; Fig. 13). During a single winter storm, considerable

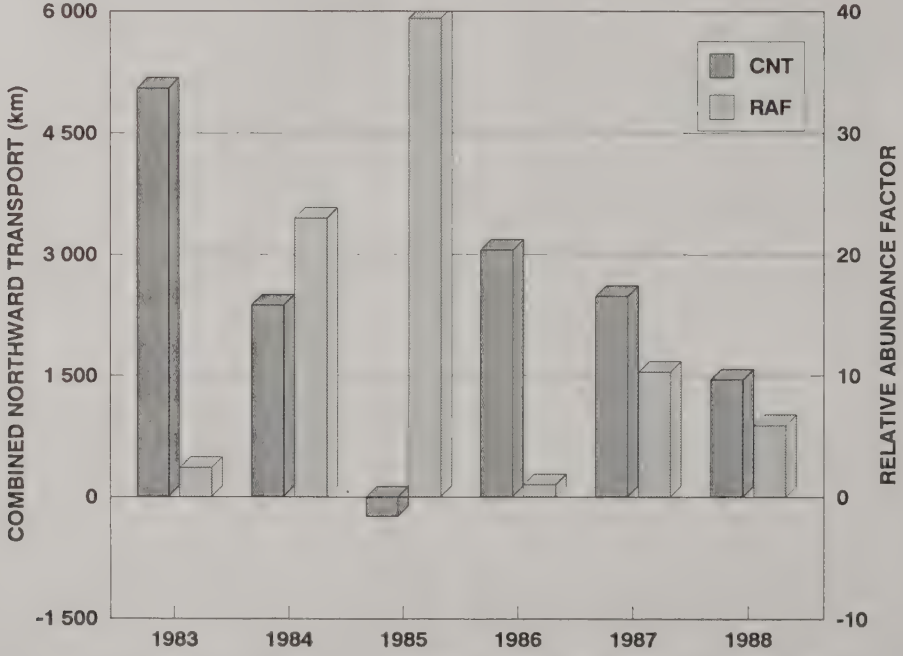

FIG. 14. Comparison between Dungeness crab settlement magnitude and total northward transport during the pelagic larval phase. The relative abundance factor (RAF) is a ratio of mean young-of-the-year abundance during June–September of the indicated years to the period of lowest abundance (1986). Combined northward transport (CNT) is the sum of geostrophic transport and the alongshore component of Ekman transport during the preceding January–May pelagic larval phase. Note the apparent inverse relationship between RAF and CNT.

alongshore transport can occur, as indicated by two oceanographic buoys which broke loose from moorings near the mouth of the Columbia River during February 1991 and travelled 250 km northward in just 2 d; transport was along isobaths (35 m) and continuous to at least the Juan de Fuca Strait (unpubl. data). Under these circumstances, Washington larvae could easily be carried beyond the functional limits of the (California–Oregon–Washington) coastal system and subsequent repatriation is unlikely. Temporary reversal of surface waters in the Juan de Fuca Strait, related to the passage of storm fronts (Thomson 1981; Hickey et al. 1991), may introduce coastal crab larvae into that system (Orensanz and Gallucci 1988; DeBrosse et al. 1990). Indeed, two of the rogue buoys from the Columbia River entered the Strait. However, once larvae traverse the Juan de Fuca Strait and become entrained in strong (and uninterrupted) northward flow off Vancouver Island (Thomson et al. 1989), they are, for all intents and purposes, lost to the coastal Washington system. (A third rogue buoy was discovered on Dundas Island, B.C. (54°33′N, 130°50′W), more than 1000 km from its original moorage near the Columbia River.) Whether coastal Washington larvae act as a source of recruits for more northern populations under these circumstances or simply perish is presently unknown. Frontal barriers to cross-shelf transport of megalopae near Vancouver Island (Jamieson et al. 1989) suggest that the latter alternative may be realized in at least some years.

From one perspective, the persistence of landward and northward transport during the winter months, coupled with proximity to high-risk areas to the north, suggests that Washington *C. magister* populations are frequently dependent on larvae originating to the south. Efford (1970) described recruitment based on alongshore transport as a process whose efficiency decreases with distance from the source. As such, the relative success of this process could depend on both the intensity and frequency of storm-related transport events. A high level of winter storm activity, accompanied by strong northward winds and currents, may deplete the coastal larval pool from which Washington recruits are drawn. Strong northward transport associated with winter storms, when integrated over the full larval period, could easily transport larvae spawned during January off central California beyond coastal Washington waters by May (Fig. 12). Drift-bottle studies have demonstrated that continuous flow exists between California and British Columbia (Hickey 1979). However, a major fraction of northward transport occurs during the month of January (mean 48% of winter total; Fig. 12) and larvae spawned after this time will experience substantially reduced northward (and greater southward) transport through ontogeny. As a result, late-hatching larvae may constitute the primary source of recruits (albeit reduced) to northern populations during years with substantial winter storm activity (e.g. 1983, 1986). Relatively strong recruitment in coastal Washington, on the other hand, may be the result of recurrent settlement by southern larvae following winters with nominal alongshore transport (e.g. 1984, 1985).

For those larvae not flushed entirely from the coastal system (i.e. beyond the Juan de Fuca Strait), there remains the possibility for recruitment following the spring transition to southward mean flow (Fig. 11). Under certain circumstances, this process may include larvae spawned along the Washington coast. Geostrophic flow reverses from northward to southward during late March/early April, as much as 1–2 mo prior to seasonal changes in local wind patterns (Hickey and Pola 1983; Strub et al. 1987; see also 1985 in Fig. 12). This phenomenon reflects remote forcing of currents by equatorward winds off northern California via coastal trapped waves (Hickey 1989). Mean winds during the April–May transition are oriented such that landward (Ekman) transport of surface waters continues during this interval (Fig. 10; Table 2), providing a mechanism for cross-shelf transport (and potential settlement) of "returning larvae". Tidally forced internal waves may also be important in this regard (Shanks 1983, 1986). Although a relationship between settlement magnitude and southward transport during spring could not be demonstrated with our data, Jamieson et al. (1989) speculated that an influx of Vancouver Island larvae spun south by the Juan de Fuca Eddy may have augmented recruitment along the Washington coast in 1985.

Additional factors may reduce the larval pool during years of protracted alongshore transport. Seaward diffusion of larvae may increase due to turbulent mixing associated with storm activity, effectively reducing larval densities in downstream settlement areas. (If moved sufficiently far offshore, larvae could conceivably cycle southward via the California Current.) Given the vulnerability of crustacean larvae to starvation (reviewed by Olson and Olson 1989), it is conceivable that weak recruitment during years of strong northward transport may, at least in part, be attributable to poor larval survival. Strong winds which deepen the mixed layer may reduce food concentrations below a critical minimum required for survival (Lasker 1975, 1978; Incze et al. 1987; Peterman and Bradford 1987). Taken together, transport-related losses of larvae may be compounded (or perhaps superceded) by starvation during periods of high storm activity.

Our conclusions are obviously constrained by the brevity of the time series. However, a similarly strong ($P < 0.01$) inverse relationship between northward transport and time-lagged commercial landings for coastal Washington during 1951–90 (McConnaughey 1991) provides corroborative evidence to support the basic result. Although cross-shelf transport distances calculated here are in excess of those required to carry newly hatched larvae close to shore for settlement, it should be remembered that boundary conditions imposed by the shoreline were not applied. Downwelling at the coast is associated with landward movement of surface waters and, although arguable, it is unlikely that larvae are subducted and transported seaward at depth (Zeldis and Jillett 1982). Downwelling velocities (approximately $0.01\ \text{cm}\cdot\text{s}^{-1}$) are well below surface-oriented swimming speeds for *C. magister* zoeae and megalopae (approximately $1–10\ \text{cm}\cdot\text{s}^{-1}$; Jacoby 1982). However, in the event of subduction and seaward transport, perhaps as a consequence of reduced activity at ecdysis, the persistence of the landward transport would serve to repeatedly cycle larvae positioned in near-surface waters back close to shore (cf. the mechanism proposed for retention of copepod populations in the Oregon nearshore by Peterson et al. (1979)).

Given the caveats stated above, it may be possible to anticipate relatively weak *C. magister* year classes along the Washington coast using readily available (and suitably corrected) ocean transport indices. Poor settlement and, consequently, declining commercial stocks may follow sustained northward transport of surface waters during the pelagic larval phase. Strong year classes, on the other hand, may follow winters characterized by significant onshore and minimal northward transport. It should be recognized, however, that successful settlement is one among numerous factors which ultimately determine the level of recruitment to the fishery; under certain circumstances, year class strength may not become fixed until the beginning of the second (1+) year (Gunderson et al. 1990; McConnaughey 1991).

Conclusions

(1) Settlement of *C. magister* megalopae along the Washington coast, as indicated by the distribution of early instars, was confined to a relatively narrow (~15 km) band in the nearshore and in estuaries. Within this coastal settlement zone, 0+ crab density generally decreased as substrate coarseness increased.

(2) The prevailing model of *C. magister* larval dynamics (involving progressive seaward transport) appears inconsistent with cross-shelf circulation of near-surface waters during the pelagic larval phase and does not account for characteristically strong alongshore (geostrophic) currents during this period. This paradigm may be an artifact of limited sampling in nearshore waters less than 50 m deep. Consequently, an intensive larval sampling program which extends into these nearshore waters should be initiated.

(3) Persistent and spatially continuous northward (wind-driven and geostrophic) flow along the U.S. west coast suggests that Washington *C. magister* populations are frequently dependent on larvae originating to the south. High storm activity and correspondingly strong alongshore transport may deplete the larval pool from which Washington recruits are drawn, resulting in poor year classes; late-hatching larvae may be particularly important during these years. Strong year classes may follow larval periods characterized by reduced alongshore transport, although factors influencing juvenile survival may also be important to subsequent fishery production.

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Egg Weight, Fecundity, and Gonad Weight Variability among Northwest Atlantic Herring (*Clupea harengus*) Populations

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Egg weight varies among northwest Atlantic herring (*Clupea harengus*) populations that spawn in different seasons ($n = 12$), but the range in weights is less than half of that known for northeast Atlantic populations. Egg weights were similar for both spring (May–June)- and autumn (August–October)-spawning herring (1.06 ×) and most dissimilar between spring- and summer (July)-spawning herring (1.21 ×). Mean population egg weights were not correlated with temperature either at spawning or for the last 2 mo of the egg development period. The product of egg weight and fecundity (standardized to length) differed between spring- and autumn-spawning herring of the southern Gulf of St. Lawrence. Spring-spawners, particularly smaller fish (≤320 mm), have lower ripe ovary weights than do autumn-spawning herring. Differences between spawning seasons in the relative allocation of storage energy to gonad and metabolism, a process mediated by the duration of the gonad maturation period, are the likely basis for the observed patterns.

Chez le hareng atlantique (*Clupea harengus*) du nord-ouest, le poids des oeufs varie selon les différentes populations qui fraient en différentes saisons ($n = 12$), mais l'intervalle de variation du poids est moins de la moitié de l'intervalle correspondant chez les populations du nord-est de l'Atlantique. Le poids des oeufs produits par les harengs qui fraient au printemps (mai–juin) est semblable à celui des oeufs pondus par les harengs qui fraient en automne (août-octobre) (1,06 ×); les plus grands écarts sont observés entre le hareng qui fraie au printemps et celui qui fraie l'été (juillet) (1,21 ×). Il n'y a pas de corrélation entre le poids des oeufs des populations moyennes et la température, que ce soit au moment de la fraie ou au cours des deux derniers mois du développement des oeufs. Le produit du poids des oeufs et de la fertilité (normalisée en fonction de la longueur) n'était pas le même selon qu'il s'agissait de harengs frayant au printemps ou de harengs frayant l'automne dans la partie sud du golfe du Saint-Laurent. Ceux qui fraient le printemps, notamment les sujets les plus petits (≤ 320 mm) ont des ovaires à maturité dont le poids est inférieur à ceux du hareng qui fraie l'automne. Il est probable que le régime de variations observé est attribuable à des différences d'une saison à l'autre dans l'utilisation relative de l'énergie en réserve par les gonades et pour le métabolisme; ce mécanisme est régulé par la durée de la période de maturation des gonades.

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Individual Atlantic herring (*Clupea harengus*) populations in the north Atlantic spawn within the same, relatively brief 4- to 6-wk period every year (Blaxter 1985; Chadwick and Claytor 1989), but as a species, herring spawn throughout the year (Iles and Sinclair 1982; Sinclair and Tremblay 1984). Mean population egg weight varies by a factor of ≈3.5 and fecundity (eggs per fish; Messieh 1976) varies by a factor of ≈4 among northeast Atlantic populations (Hempel and Blaxter 1967; Sinclair and Tremblay 1984). These reproductive traits vary inversely, with winter–spring (December–March)-spawning herring having larger but fewer eggs than summer–autumn (June–September)-spawning herring (Blaxter and Hempel 1963; Mann and Mills 1979; Sinclair and Tremblay 1984).

Seasonal variability in both egg weight and fecundity in herring and their seasonal inverse relationship have generally been interpreted as evidence for a link between survivorship during the early life history and the reproductive traits of fishes. This "trade-off" (Mann and Mills 1979) is thought to enhance survival as biological and oceanographic conditions vary with season (Hempel 1965; Blaxter and Hempel 1966; Cushing 1967; Mann and Mills 1979; Sinclair and Tremblay 1984; Blaxter 1985; Rothschild 1986; Miller et al. 1988; Bailey and Houde 1989). Implicit in this hypothesis is that for fish with the same body size but from different populations, mature gonad weight (i.e. the realized reproductive effort) is assumed to either be constant (Ware 1975; Mann and Mills 1979; Wootton 1979; Tanasichuk and Ware 1987; Duarte and Alcarez 1989) or vary to a lesser extent than does either egg weight or fecundity (Hempel 1965; Sinclair and Tremblay 1984; Blaxter 1985). However, these assumptions have not always been verified, and the influence of variability in gonad weight on predictions from theory of changes in reproductive traits with season is unknown (Tanasichuk and Ware 1987).

Similar patterns of variability in reproductive traits have been assumed for northeast (NE) and northwest (NW) Atlantic herring populations (e.g. Ware 1975; Lett and Kohler 1976; Winters and Wheeler 1987) on the basis that autumn-spawners are also more fecund than spring-spawners in the NW Atlantic (Hodder 1972; Messieh 1976; Messieh et al. 1979a, 1985; Kelly and Stevenson 1985; Bradford 1987). However, neither mature egg weights nor gonad weights have been reported for NW Atlantic herring.

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True winter (December–March)-spawning herring, which account for much of the seasonal variability in both egg weight and fecundity in the NE Atlantic (Blaxter 1985; Almatar and Bailey 1989), are absent in the NW Atlantic (Colton et al. 1979; Haegele and Schweigert 1985). Therefore, reduced variability in reproductive traits among NW Atlantic populations is possible. However, the same approximate 11°C range in water temperatures between the "spring"- and "autumn"-spawing seasons is evident for both NE and NW Atlantic herring (Haegele and Schweigert 1985; Bradford 1991). Therefore, and in contrast, a comparable degree of variability in reproductive traits among both NE and NW Atlantic populations is also possible, assuming that egg weight is inversely correlated with water temperature (e.g. Bagenal 1971; Ware 1975; Mann and Mills 1979; Markle and Frost 1985; Tanasichuk and Ware 1987).

Life history differences between NE and NW Atlantic herring further complicate direct comparisons of reproductive traits. Adult NW Altantic herring are large bodied (asymptotic length (L_∞) $\geqslant$ 33 cm; Messieh and Tibbo 1971; Anthony and Waring 1980) and relatively long lived ($\text{age}_{\max} \approx 20$; Lea 1929). Both body size and life span are highly variable among NE Atlantic populations (21 cm $\leqslant L_\infty \leqslant$ 37 cm, 10 $\leqslant \text{age}_{\max}$ (years) $\leqslant$ 23; Parrish and Saville 1965; Cushing 1967; Blaxter 1985; Parmanne 1990), particularly among populations with different spawning seasons (Beverton 1963; Cushing 1967; Blaxter 1985). Consequently, life history traits differ among populations with the same spawning time but from different regions of the north Atlantic. May–June-spawning NW Atlantic herring are larger (L_∞ = 33 versus 21 cm) and longer lived ($\text{age}_{\max}$ = 20 versus 10 yr) than May–June-spawning Baltic Sea herring. Because fecundity and, for some populations, egg weights are strongly positively correlated with body size (Hempel and Blaxter 1967; Blaxter 1985), differences in herring reproductive traits among regions are possible.

In this paper, we use egg weight, fecundity, and gonad weight data from NW Atlantic herring populations to investigate variation in egg weight among spring-, summer-, and autumn-spawning populations. We also test whether egg weight is correlated with water temperature, whether egg weight varies inversely with egg number between spring- and autumn-spawning NW Atlantic herring, and whether gonad weight, for a given body size, is constant among populations that spawn during different seasons.

Materials and Methods

Data Base and Selection of Common Measure of Body Size

Simultaneous estimates of egg weight, absolute fecundity, and ripe gonad weight are not obtainable for individual fish. Ripe fish with freely extruded, fully mature eggs provide the best measure of egg weight but unreliable measures of both fecundity and gonad weight. Mature fish in near-spawning condition, which do not extrude their eggs, provide good measures of fecundity and a close approximation of mature gonad weight but underestimates of egg weight.

We used four data sets to examine variation in herring reproductive traits among spring-, summer-, and autumn-spawning NW Atlantic populations. Egg weight estimates for ripe individuals from 12 populations representing both the full range of herring spawning times and the herring's southern and central range in the NW Atlantic (Leim and Scott 1966; Haegele and Schweigert 1985) were used to determine how egg weight varied among herring which spawned during different seasons. Two other data sets, one consisting of egg weight estimates and the other of fecundity estimates, for the spring- and autumn-spawning southern Gulf of St. Lawrence (southern Gulf or NAFO Subdivision 4T) herring populations were used to test whether egg weight and fecundity vary inversely among populations. The fourth data set consisted of gonad weights and fish lengths for individual mature female herring from three spring-spawning, one summer-spawning, and two autumn-spawning NW Atlantic herring populations. These data were used to test whether gonad weights for a common body size varied among populations with different spawning seasons.

Total length was the only suitable common measure of body size for this study because weight varies differently among populations which spawn during different seasons. Most herring, including those in the NW Atlantic, use somatic energy stores to simultaneously develop gonad and fulfil all routine and active metabolic requirements (Iles 1964, 1984; Parsons and Hodder 1975). Thus for spring-spawners, which develop gonads before winter (Iles 1964; Parsons and Hodder 1975; McQuinn 1989), maintenance and active metabolism during gonad maturation are synonymous with their overwintering metabolic demand (Winters 1977; Bradford 1991). In contrast, the overwintering metabolic demand of spent autumn-spawners is subsequent to the maintenance and active metabolic demand on stored energy during gonad maturation (Iles 1984; Bradford 1991). Yet the stored energy necessary to meet their metabolic demand during the fasting period (gonad maturation plus overwintering) is accumulated prior to gonad maturation (Bradford 1991). Consequently, somatic weights differ between spring- and autumn-spawning NW Atlantic herring completely independently of the relative allocation of energy to gonads and soma (Bradford 1991). In contrast, fish length, an accepted standard measure for body size (Lee 1912; Lea 1929; Iles 1974; Parmanne 1990), does not change either during gonad maturation and/or in winter conditions for Atlantic herring (Lee 1912; Lea 1929; Iles 1974; Bradford and Iles 1992).

Herring Egg Weight Variability among Seasons, among Populations, and in Relation to Water Temperature

Fully mature female herring ("ripe and running," maturity stage 6; Anonymous 1962) were collected between April and October 1986 from 12 commercial fisheries (Fig. 1). Following previous designations (Leim and Scott 1966; Messieh and Tibbo 1971; Haegele and Schweigert 1985), herring spawning from early April to late June (Bras D'Or Lake, Escuminac, Miminegash, Bonavista Bay, Minas Basin), mid-July to early August (Ile Haute, eastern Maine), and mid-August to late October (southwest (SW) Nova Scotia, German Bank, Grand Manan, Western Bank, Georges Bank) were defined as spring-, summer-, and autumn-spawners, respectively. Both random and length-stratified samples of fish were obtained from each fishery. These ensured an adequate representation of the full range in body size of adult herring from each population. All samples were frozen within 2–3 h of capture and stored for $\leqslant$6 mo.

In the laboratory, fish were thawed and their total length (millimetres) measured. Ovaries were removed, weighed (to the nearest 0.01 g), and a subsample of ovary from each female stored in Gilsons solution (Bagenal 1978) for at least 6 mo.

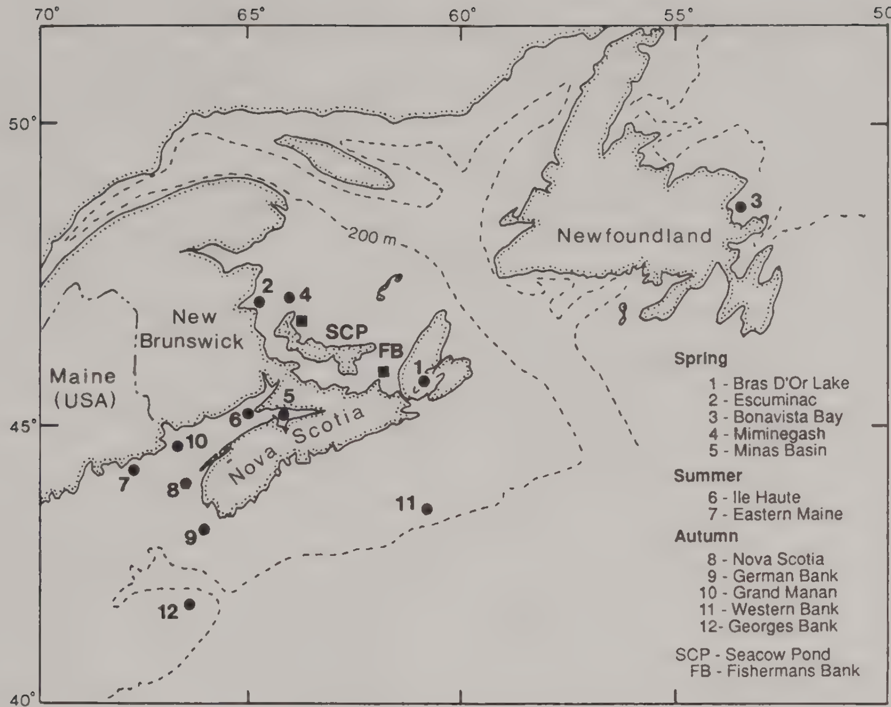

FIG. 1. Map of NW Atlantic region from which samples were obtained for egg weight determinations.

This preparation fixes ripe eggs and allows for their separation from the surrounding ovarian tissue. Upon removal from the Gilsons solution, each section of ovary was placed in a 1-L beaker filled with fresh water. Eggs were liberated by gentle finger pressure on the ovary section and the ovary material removed by repeated rinsings with tap water. Eggs were transferred to small glass jars and soaked in deionized water for ≈1 h.

Three subsamples from each jar were placed in preweighed dishes and their egg number counted under a dissecting microscope at 12× magnification. Subsamples in which ovary tissues were still attached to the eggs were discarded. Broken or atretic eggs (misshapen, grossly hydrated; Bowers and Holliday 1961) were removed. Most of the subsamples contained between 250 and 750 eggs. Samples that did not provide three subsamples with ≥250 eggs each were discarded because preliminary analysis showed that the estimated mean egg dry weight estimates obtained with smaller subsamples were inaccurate. All subsamples were dried for 48 h at 40°C, cooled to room temperature in a desiccator, and reweighed (to the nearest 0.0001 g). Mean egg dry weight (referred to hereafter as egg weight) of the three subsamples was used as the measure of egg weight for each fish (<3% variability among subsamples).

Least squares linear regressions were calculated for population mean egg dry weights versus monthly mean sea surface temperatures (degrees Celsius). The water temperatures used were for the hydrographic subregions described by Drinkwater and Trites (1988) which correspond to the location of the spawning grounds. The influence of temperature both at the time of spawning and 60 d prior to spawning, as suggested by Tanasichuk and Ware (1987), was examined.

Egg Weight and Fecundity Variability between Spring- and Autumn-Spawning Southern Gulf of St. Lawrence Herring

Herring from the southern Gulf were collected fresh from commercial gillnet catches during May (years 1988 and 1989) in the vicinity of Seacow Pond, P.E.I., and during August–September from Fishermans Bank, P.E.I. (Fig. 1). Ripe females (maturity stage 6; Anonymous 1962) were selected at random from the catch and total length (millimetres) was measured. Several thousand eggs were stripped from each female into individual vials containing Gilsons solution and stored for ≥6 wk. Two subsamples of preserved eggs (400–800 eggs each) were then rinsed, dried, and counted as described above. Replicates differed in dry weight by <5%.

Mature (maturity stage 5; Anonymous 1962) female herring were also collected from the Seacow Pond and Fishermans Bank fisheries. Ovaries were removed from each fish, weighed (to the nearest 0.01 g), and then placed in glass jars with Gilsons solution. Samples were stored for ≥6 wk to break down the ovarian tissues encapsulating the eggs. Mature eggs were collected and counted using the rapid wet weight procedure described by Bradford and Iles (1992). This procedure produces fecundity estimates that are both repeatable and comparable with those obtained using other established procedures (Bradford 1987). Absolute fecundity (F_a) was calculated as

(1) $F_a = W_e \cdot X_n$

where W_e = wet weight (grams) or egg mass and X_n = mean number of eggs per gram for three subsamples.

Additional fecundity determinations for southern Gulf spring- and autumn-spawning herring were obtained from Dr. D. Cairns (Department of Fisheries and Oceans, Moncton, N.B.). The analytical procedures for these samples (Messieh 1976) were similar to those for the present study except that the separated eggs were dried at 50°C for 24 h prior to subsampling. This method produces estimates of fecundity comparable with those used in the present study (Bradford 1987). The fecundity data for all years (1969–88 inclusive) were pooled.

Among-Population Variability in Ovary Weight

Records of mature female herring (maturity stage 5), obtained by routine port sampling of commercial fisheries, were used to determine gonad weight variability both between and within populations. Information available for each fish included location and date of capture, gear type, total length (millimetres), total weight (to the nearest 0.1 g), and gonad wet weight (to the nearest 0.01 g). Samples were obtained from six "spawning" fisheries, each of which is currently recognized as a discrete spawning unit (Sinclair et al. 1985) and which collectively represent the known spawning times for herring in the NW Atlantic. These include Bras D'Or Lake (April), southern Gulf spring (May–June), Minas Basin (May–June), Ile Haute (July–August), southern Gulf autumn (August–September), and SW Nova Scotia autumn (August–September) (Fig. 1).

Fish ≤275 mm were excluded because of gillnet selectivity (Hamley 1975; Winters and Wheeler 1990). Fresh total length (millimetres) for each fish was calculated from the empirical relationship (Hunt et al. 1986)

$$(2)\quad L_{\text{fresh}} = 2.28 + 1.01 \cdot L_{\text{frozen}} \qquad (r^2 = 0.99)$$

where L_{fresh} = fresh length and L_{frozen} = frozen length (millimetres). Ovary weight was related to total length for each spawning group over a common length range (275–350 mm) using least squares regression of the $\log_e$-transformed data.

Results

Herring Egg Weight Variability among Seasons, among Populations, and in Relation to Water Temperature

Egg weight – fish length regressions showed no significant relationship for 10 of the 12 populations with the exception of spring-spawners (Bonavista Bay: df = 37, r^2 = 0.50, $P < 0.001$; Minas Basin: df = 29, r^2 = 0.20, $P < 0.01$). Therefore, analysis of variance (ANOVA) was used for comparisons among populations and among seasons. Egg weights differed statistically among populations (ANOVA: df = 11,429, F = 30.15, $P < 0.001$), but spring-spawned eggs were only marginally heavier (1.06×) than autumn-spawned eggs (pooled mean egg weights ± 1 SD were 14.91 ± 2.56 mg/100 eggs (n = 160) and 14.01 ± 1.50 mg/100 eggs (n = 193), respectively). A seasonal change, although evident (ANOVA a posteriori contrasts; Fig. 2), was also weak with both spring- and autumn-spawned eggs heavier by 1.21× (df = 1,428; F = 142.1; $P < 0.001$) and 1.13× (df = 1,428, F = 37.7, $P < 0.001$), respectively, than summer-spawned eggs (12.35 ± 1.47 mg/100 eggs (n = 113)).

Differences in egg weights between individual populations were small (maximum range = 1.43× for Bras D'Or Lake (spring) and eastern Maine (summer); Fig. 2). Eighteen of 30 possible spring–autumn comparisons differed significantly ($P < 0.05$; Tukeys multiple between-group comparison test, adjusted for unequal sample sizes (Zar 1984) (Table 1). Eight of 10 possible spring–summer and 10 of 12 possible summer–autumn comparisons differed significantly (Table 1). Egg weights did not vary with sampling date for SW Nova Scotia autumn-spawning herring (SW Nova Scotia I and II sampled 34 d apart; Table 1).

Mean egg dry weight was not correlated with either the monthly mean sea surface temperature at spawning (df = 11, r = 0.42, $P > 0.05$; Fig. 3A) or 60 d prior to spawning (df = 11, r = 0.30, $P > 0.05$; Fig. 3B).

Egg Weight and Fecundity Variability between Spring- and Autumn-Spawning Southern Gulf of St. Lawrence Herring

Autumn-spawning herring were more fecund than spring-spawning herring (Fig. 4; ANCOVA: df = 1,1,503, F_{season} = 231.91, F_{length} = 443.27, $P_{\text{season}} = P_{\text{length}}$ = 0.0001). Both the intercepts and the slopes of the ln-transformed absolute fecundity – length regressions (Fig. 4) were significantly different (df = 1,504, F = 232.22, $P < 0.0001$ and df = 1,503, F = 8.56, $P < 0.01$, respectively; Sokal and Rohlf 1981; Zar 1984). Fecundity differences between southern Gulf spring- and autumn-spawning herring decreased with length (1.76 and 1.39× at 275 and 345 mm, respectively, according to predicted fecundity–length relationships from Fig. 4).

Egg weight (W) increased with female length (L) for spring-spawning herring (P = 0.001; Fig. 5) but showed no relationship with length for autumn-spawning herring ($P > 0.05$; Fig. 5). Two-way ANOVA revealed a significant interaction between spawning season and year of sampling (df = 1,426, F = 38.35, $P < 0.001$). No difference in egg weight (Table 2) was detectable either between seasons (df = 1,1, F = 7.80, $P > 0.20$) or between years (df = 1,1, $F < 1.0$, $P > 0.50$) using the interaction term as the denominator for tests of significance of the main effects.

Among-Population Variability in Ovary Weight

Gonad weights varied among populations (ANCOVA: df = 5,1,934, F_{group} = 117.52, F_{length} = 1630.63, $P_{\text{group}} = P_{\text{length}}$ = 0.0001), with differences in both the intercepts and slopes of the ln-transformed fecundity–length regressions (df = 5,940, F = 117.97, $P < 0.001$ and df = 5,935, F = 21.02, $P < 0.001$, respectively; Sokal and Rohlf 1981; Zar 1984). In general, ovary weight variability among populations was greater at shorter lengths than at longer lengths over the common length interval (by 21.6 and 5.6 g at 275 and 350 mm, respectively between 4T spring and SW Nova Scotia; Fig. 6).

The gonads of autumn-spawning fish were the heaviest of all the groups examined (Fig. 6). Between-population differences (Tukey's multiple comparison test at $P < 0.01$, adjusted for unequal sample sizes), defined as differences in either slopes or intercepts or both (Zar 1984), were organized as follows. Five of six spring–autumn comparisons (not Bras D'Or Lake – 4T autumn) showed significant differences (Table 3). Two of three spring–summer comparisons (not Bras D'Or Lake – Ile Haute) showed significant differences (Table 3). One of two summer-autumn comparisons (not Ile Haute – SW Nova Scotia) showed a significant difference (Table 3). The relationships for Bras D'Or Lake (April) and Minas Basin (May–June) herring are statistically the same (Table 3).

Spring to autumn ratios of both wet ovary weight and a dry ovary weight index (fecundity·dry egg weight) at length showed

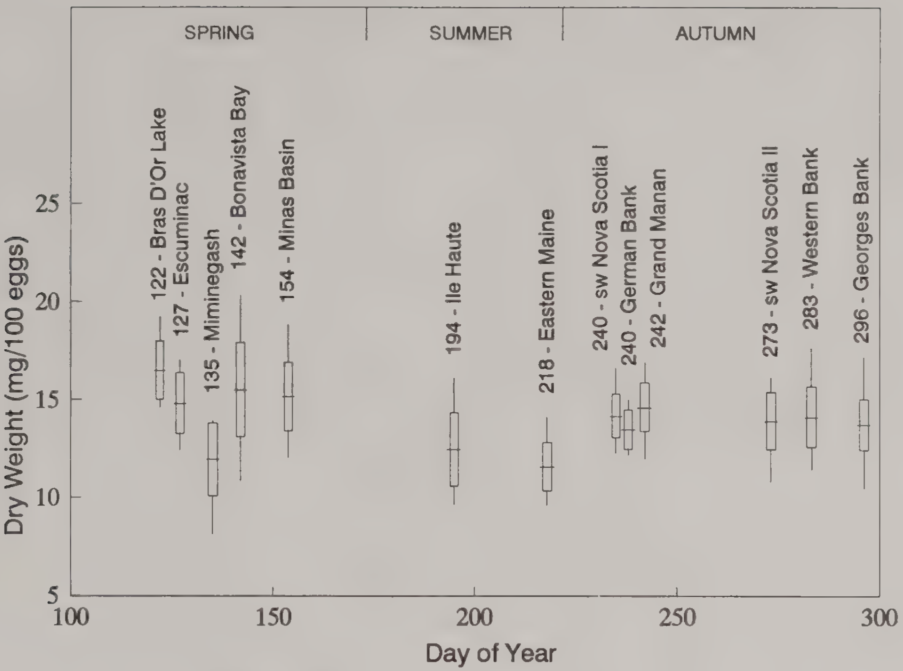

FIG. 2. Mean (point), standard deviation (box), and range (line) of egg weight for NW Atlantic herring populations versus day of capture (day). The number before the name of each population is the day of capture.

TABLE 1. Tukey's multiple between-group comparison test adjusted for unequal sample sizes at $P < 0.05$ (N.S. = no significant difference; significantly different comparisons are ○ = summer versus autumn, ● = summer versus spring, □ = spring versus autumn, and ■ = spring versus spring).

	Eastern Maine	Miminegash	Ile Haute	German Bank	Georges Bank	SW Nova Scotia II	Western Bank	SW Nova Scotia I	Grand Manan	Escuminac	Minas Basin	Bonavista Bay
Eastern Maine	—											
Miminegash	N.S.	—										
Ile Haute	N.S.	N.S.	—									
German Bank	○	□	N.S.	—								
Georges Bank	○	□	N.S.	N.S.	—							
SW Nova Scotia II	○	□	○	N.S.	N.S.	—						
Western Bank	○	□	○	N.S.	N.S.	N.S.	—					
SW Nova Scotia I	○	□	○	N.S.	N.S.	N.S.	N.S.	—				
Grand Manan	○	□	○	N.S.	N.S.	N.S.	N.S.	N.S.	—			
Escuminac	●	■	●	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	—		
Minas Basin	●	■	●	□	□	N.S.	N.S.	N.S.	N.S.	N.S.	—	
Bonavista Bay	●	■	●	□	□	□	□	N.S.	N.S.	N.S.	N.S.	—
Bras D'Or Lake	●	■	●	□	□	□	□	□	□	■	N.S.	N.S.

that the total investment into gonads is greater for autumn-spawners than for spring-spawners in the southern Gulf (Fig. 7). Both ratios remained greater than 1 over the common length range (270–350 mm), but between-group differences became less extreme with fish length (Fig. 7). These patterns of variability for both gonad weight and the reproductive index were the same as for absolute fecundity which also differed less extensively between southern Gulf spring- and autumn-spawning herring with length (see above).

Discussion

Egg weight variability among NW Atlantic herring populations (1.43 ×) is less than one half of the egg weight variability

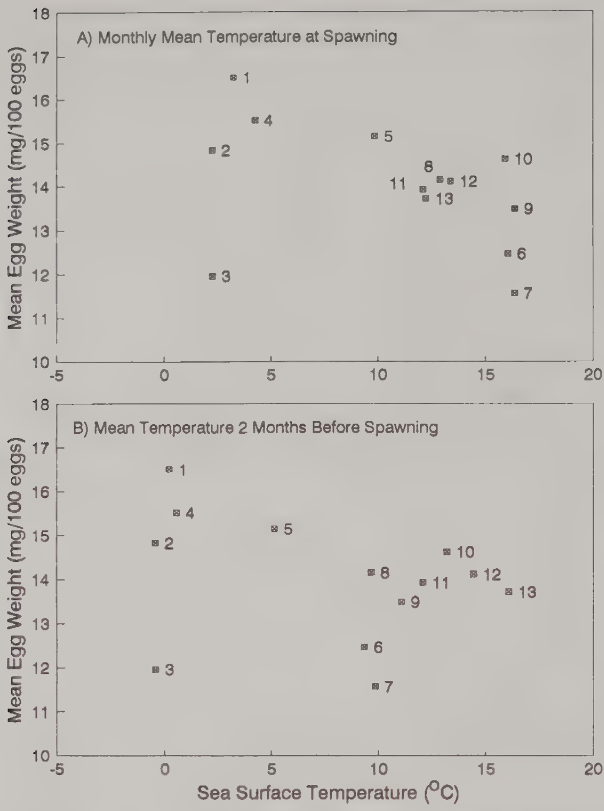

FIG. 3. Mean population egg weight versus the mean monthly temperature corresponding to (A) the spawning period, and (B) 2 mo before spawning. Populations are numbered according to their location on Fig. 1 and their order from left to right in Fig. 2.

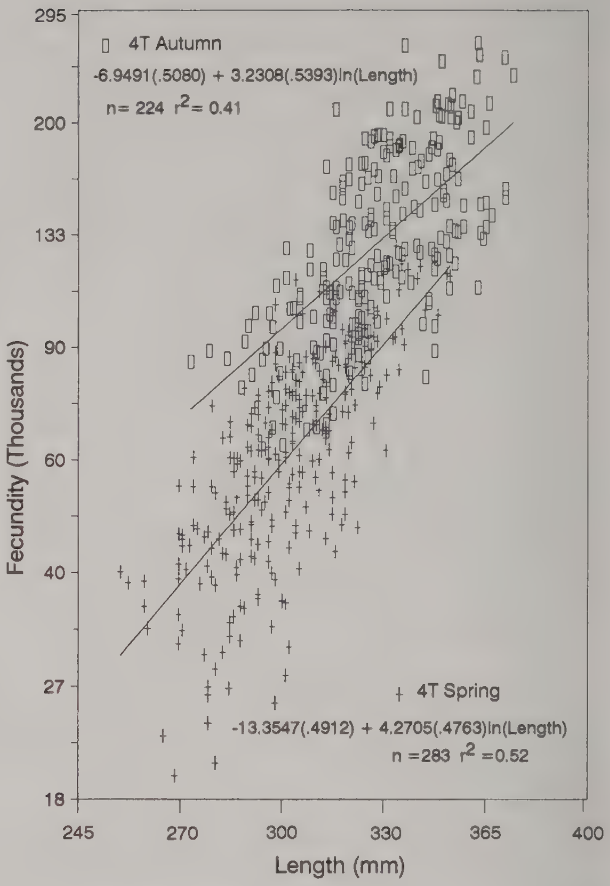

FIG. 4. Relationship between fecundity (ln absolute) and length (ln) for spring- and autumn-spawning southern Gulf of St. Lawrence herring (years of sampling: 1969–1988). The 95% confidence intervals of the regression parameters are given in parentheses for each equation.

among NE Atlantic populations (≈3.5 ×; Hempel and Blaxter 1967; Sinclair and Tremblay 1984). The lightness of summer-spawned eggs, relative to the other seasons, accounts for the weak seasonal trend, with only minor differences between these eggs and the slightly heavier spring (1.21 ×)- and autumn (1.13)-spawned eggs. The differences in egg weight between spring and autumn have questionable biological significance (1.06 × for pooled spring- and pooled autumn-spawning groups; no difference between southern Gulf spring- and autumn-spawners pooled across years). These results contradict predictions that populations which have the same spawning season will have similar egg weights (Ware 1975) as well as the assumption that seasonal variability in egg weight is comparable for both NE and NW Atlantic populations (Lett and Kohler 1976; Winters and Wheeler 1987). As a consequence, the terms "spring-spawning" and "autumn-spawning," which accurately summarize local spawning environments, do not embody the same physiological connotation for all populations throughout the herring's geographic range. Herring reproductive traits from one region of the north Atlantic are not necessarily applicable to herring from other regions even when populations that spawn during the same time are compared.

Direct comparisons of egg weights between NE (from Hempel and Blaxter 1967) and NW Atlantic are not advisable because of the unknown relative effects of different egg preservation methods (i.e. Gilsons solution versus a formalin–seawater solution). However, indirect comparisons are possible. Predicted dry weights for unspawned eggs from average-sized (325 mm) southern Gulf spring- and autumn-spawning herring are 16.6 and 13.3 mg/100 eggs, respectively (from their fecundity–length and gonad–length relationships and assuming a moisture content of 75% for ripe ovary tissue (McGurk et al. 1980; R. G. Bradford, unpubl. data)). These estimates are comparable (ignoring the weight of ovary tissue) with those reported by Hempel and Blaxter (1967) for August–September-spawning Buchan herring (≈16 mg/100 eggs) of the North Sea but lower by >2 × than those of March ("spring")-spawning Norwegian herring (34.5 mg/100 eggs). Therefore, the different patterns of egg weight variability are partly due to the absence from the NW Atlantic of (large egg) winter-spawning herring.

Water temperature appears to play only a minor ecological role in the determination of egg weight in NW Atlantic herring. Herring egg weight is not correlated with water temperature in the NW Atlantic (Fig. 3). Furthermore, similar spawning temperature variability between populations in both NE and NW Atlantic herring (≈11°C, fig. 3, and table 1 from Haegele and Schweigert 1985) does not result in comparable among-population egg weight variability. Yet, light-weight NW Atlantic spring-spawned eggs develop in winter conditions (Hodder et al. 1973; McGurk et al. 1980; Bradford 1991) at lower temperatures (1–3°C; Winters 1977; Bradford 1991) than those reported for heavy-weight Norwegian herring eggs (4–7°C; Runnstrom 1941).

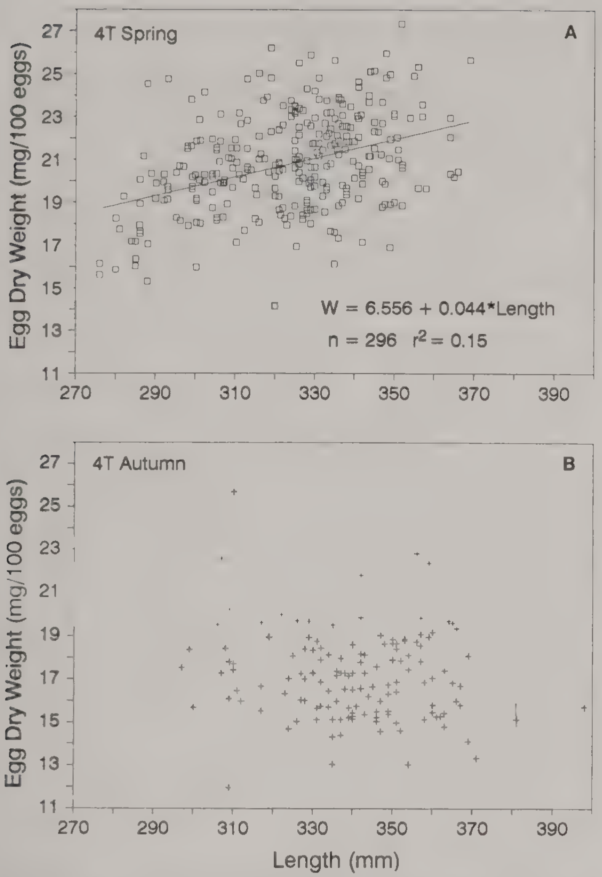

FIG. 5. Egg weight versus length for (A) spring- and (B) autumn-spawning southern Gulf of St. Lawrence herring sampled during 1988 and 1989.

TABLE 2. Mean egg weights ± 1 SD and coefficients of variation (CV) for southern Gulf (4T) spring- and autumn-spawning herring sampled during 1988 and 1989.

Season	Year	n	Mean weight (mg/100 eggs)	SD	CV
4T spring	1988	211	21.24	2.30	10.85
	1989	83	20.28	1.89	9.31
	Combined	294	20.94	2.21	10.53
4T autumn	1988	44	16.63	1.50	9.01
	1989	95	17.48	1.83	10.45
	Combined	139	17.19	1.82	10.59

Comparisons of yolk-sac larval length between spring- and autumn-spawned populations also indicate that egg weight and temperature are not strongly correlated in the NW Atlantic. In the Bay of Chaleur (southern Gulf), both spring- and autumn-spawned larvae hatch at a length of ≈5–6 mm even though water temperatures at spawning differ by as much as 10–12°C between spawning seasons (Jean 1956). Length at hatching is positively correlated with egg size (Blaxter and Hempel 1963; Miller et al. 1988; Duarte and Alcarez 1989).

The assumption that differences in fecundity (at length) between spring- and autumn-spawning NW Atlantic herring reflect differences in egg weight is not supported (e.g. Ware 1975; Lett and Kohler 1976; Winters and Wheeler 1987). Fecundity alone cannot predict egg weight. In the southern Gulf, spring- and autumn-spawned egg weights grouped across years are virtually identical (Table 2), but autumn-spawning herring (320 mm in length) are on average ≈50% more fecund than spring-spawning herring (Fig. 4).

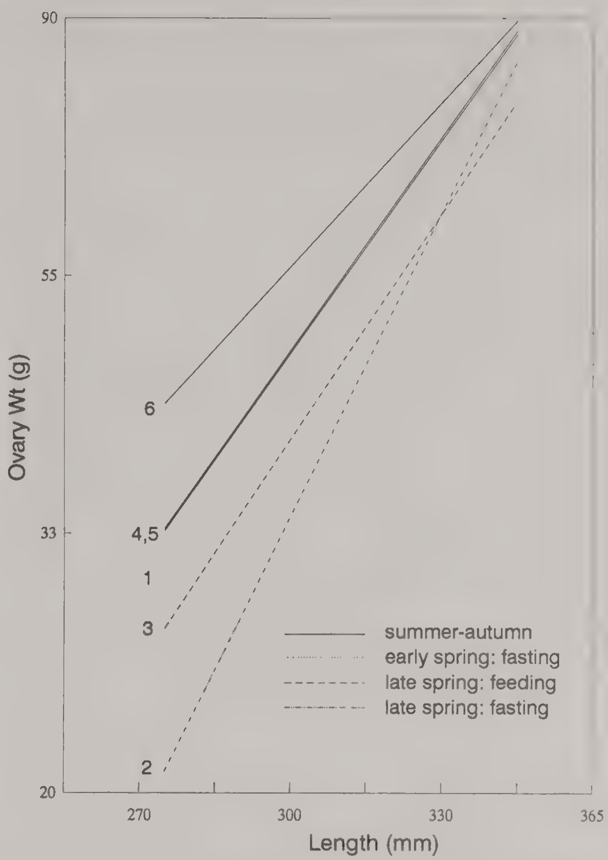

FIG. 6. Predicted relationships between gonad weight (ln) and length (ln) for summer–autumn-spawning, early spring-spawning fasting, late spring-spawning feeding, and late spring-spawning fasting NW Atlantic herring populations where 1 = Bras D'Or Lake (-21.3309 (0.3508) + 4.4086 (0.6593)$\cdot\ln(L)$, $n = 74$, $r^2 = 0.71$, $P < 0.001$), 2 = 4T spring (-30.0883 (0.4356) + 5.8985 (0.3826)$\cdot\ln(L)$, $n = 279$, $r^2 = 0.77$, $P < 0.001$), 3 = Minas Basin (-21.3006 (0.3364) + 4.3830 (0.6349)$\cdot\ln(L)$, $n = 96$, $r^2 = 0.67$, $P < 0.001$), 4 = Ile Haute (-19.7440 (0.3572) + 4.1402 (0.8075)$\cdot\ln(L)$, $n = 48$, $r^2 = 0.70$, $P < 0.001$), 5 = 4T autumn (-19.6949 (0.4555) + 4.1306 (0.7614)$\cdot\ln(L)$, $n = 144$, $r^2 = 0.45$, $P < 0.001$), 6 = SW Nova Scotia (-14.1319 (0.3359) + 3.1842 (0.3578)$\cdot\ln(L)$, $n = 300$, $r^2 = 0.51$, $P < 0.001$). Numbers in parentheses = 95% confidence intervals; L = length.

Differences in ovary weights at length among NW Atlantic populations (Fig. 6) explain the lack of a strong inverse relationship between egg weight and fecundity. Gonad weight at length differs among populations on the basis of spawning season. Summer- and autumn-spawning herring have heavier ovaries and are therefore more fecund than spring-spawning populations.

Metabolic rate declines exponentially with body size (Winberg 1961), but capacity to store surplus energy increases with body size in fishes (MacLean et al. 1981). Consequently, fishes, while fulfilling their metabolic obligations from somatic energy stores, commonly exhibit size-dependent limitations in the

TABLE 3. Tukey's multiple between-group comparison test adjusted for unequal sample sizes for slopes and intercepts of gonad weight (ln)(g) versus length (ln) of NW Atlantic herring populations. Numbers are q statistic values which differ significantly ($P < 0.05$) (N.S. = not significantly different).

		Bras D'Or Lake	4T spring	Minas Basin	Ile Haute	4T autumn	SW Nova Scotia
Bras D'Or Lake	Slope	—	5.11	N.S.	N.S.	N.S.	8.73
	Intercept	—	8.33	N.S.	N.S.	N.S.	7.01
4T spring	Slope		—	5.33	4.97	7.27	17.55
	Intercept		—	4.70	8.36	10.10	26.04
Minas Basin	Slope			—	N.S.	N.S.	8.18
	Intercept			—	4.89	5.83	13.59
Ile Haute	Slope				—	N.S.	6.55
	Intercept				—	N.S.	4.15
4T autumn	Slope					—	4.88
	Intercept					—	5.49
SW Nova Scotia	Slope						—
	Intercept						—

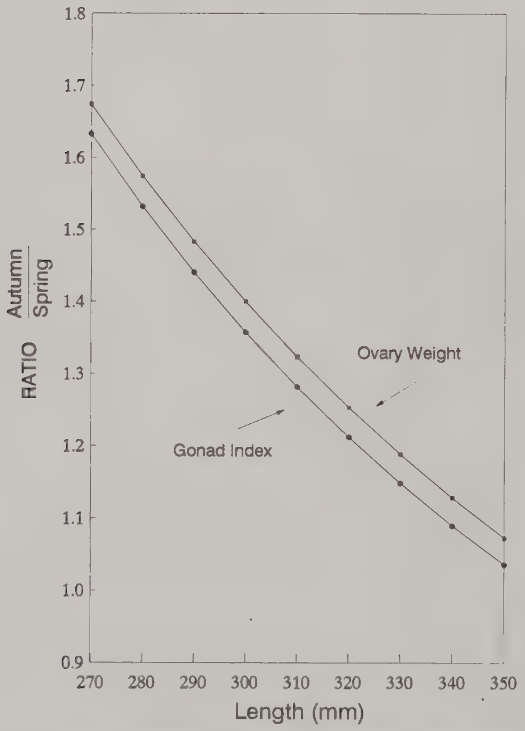

FIG. 7. Ratios of autumn- to spring-spawning ovary weights (g) (squares) and autumn- to spring-spawning reproductive index (fecundity·egg weight (mg)) (circles) versus length for southern Gulf of St. Lawrence herring.

length of time they can sustain themselves (MacLean et al. 1981). For some anadromous adult fishes, postspawning mortality (American shad (*Alosa sapidissima*), Glebe and Leggett 1981) and the annual frequency of spawning (lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedi*, previously *C. artedii*), Lambert and Dodson 1990) are a function of body size- and time-dependent constraints on storage energy utilization.

Similarly, the lower realized reproductive effort of May–June spawners in comparison with August–September spawners (Fig. 6 and 7) may be due to differences in their resistance to excessive energy depletion during gonad maturation. Few NW Atlantic spring- and autumn-spawning populations feed during gonad maturation (Parsons and Hodder 1975; Messieh et al. 1979b; Crawford 1980; but see below). For spring-spawners, with a lengthy gonad maturation period (7–9 mo, Iles 1964; Hodder et al. 1973; McQuinn 1989), nonreproductive utilization of storage energy may be greater than for autumn-spawners with a brief gonad maturation period (4 mo, Iles 1964; Hodder et al. 1973; McQuinn 1989).

Comparisons of the two May–June-spawning populations also indicate that gonad production in spring-spawners is potentially constrained by limits in the storage of surplus energy. Minas Basin herring are exceptional in that they feed intensively during the late stages of gonad maturation up to and including ovulation (Bradford 1987). In relation to length, their gonad weights (Fig. 6), fecundity (Bradford and Iles 1992), and somatic weights (Bradford and Iles 1992) are all greater than those of southern Gulf herring which fast during the final stages of gonad maturation (Parsons and Hodder 1975; Messieh et al. 1979b), but spawn at the same time (Chadwick and Claytor 1989). Furthermore, the gonad weight at length relationship for the feeding Minas Basin herring is the same as that for Bras D'Or Lake herring, but which spawn 4–6 wk earlier (Crawford et al. 1982; R. L. Stephenson, unpubl. data).

Egg weight is concluded to be a conservative reproductive trait in NW Atlantic herring. However, fecundity is highly variable between spawning seasons, showing that egg number is favoured over egg quality. Between-season differences in realized reproductive effort (gonad weight at length) account for the weak inverse relationship between egg weight and fecundity.

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Manipulation of Reproductive Function in Atlantic Salmon (*Salmo salar*) Kelts with Controlled Photoperiod and Temperature

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Johnston, C. E., M. J. Hambrook, R. W. Gray, and K. G. Davidson. 1992. Manipulation of reproductive function in Atlantic salmon (*Salmo salar*) kelts with controlled photoperiod and temperature. Can. J. Fish. Aquat. Sci. 49: 2055–2061.

Atlantic salmon (*Salmo salar*) kelts exposed to a regime of two 6-mo seasonally accelerated light increases and decreases (2CP) in 1989 spawned in the spring of 1990 when water temperatures were above 7°C during the winter months. Kelts exposed to water temperatures below 4°C during the same period failed to spawn in the spring. Exposure of the nonspawning 2CP kelts to warmer water temperatures in the summer of 1990 stimulated egg development and ovulation by 17 October 1990. Kelts exposed to a simulated natural 12-mo photoperiod regime also spawned at this time. Eggs and sperm from kelts spawned in the spring were viable. Spring-spawned eggs fertilized with fresh sperm had lower survival levels to the eyed-egg stage or to hatch than did eggs from wild fall-spawned stocks. Kelts entrained to spawn in the spring with 2CP photocycles were manipulated to spawn again in the spring of the next year following exposure to a time-shifted photoperiod and elevated winter/spring water temperature.

Des charognards de saumon de l'Atlantique (*Salmo salar*) exposés à un régime de deux photocycles de six mois à augmentation et diminution accélérées de l'éclairement (2CP) en 1989 ont frayé au printemps 1990 alors que la température de l'eau était supérieure à 7°C pendant les mois d'hiver. Les charognards exposés à des températures de l'eau de moins de 4°C pendant la même période n'ont pas frayé au printemps. L'exposition des charognards 2CP non géniteurs à des températures plus élevées à l'été 1990 a stimulé le développement des oeufs et l'ovulation au 17 octobre 1990. Les charognards exposés à un régime simulant la photopériode naturelle de douze mois ont aussi frayé au même moment. Les oeufs et le sperme des charognards qui ont frayé au printemps étaient viables. Les oeufs pondus au printemps et fécondés avec du sperme frais présentaient des taux de survis jusqu'au stade oeillé ou à l'éclosion plus bas que les oeufs des stocks sauvages frayant à l'automne. Les charognards amenés à frayer au printemps avec les photocycles 2CP ont été manipulés et amenés à frayer de nouveau au printemps de l'année suivante après exposition à une photopériode artificielle et à une température élevée de l'eau en hiver et au printemps.

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Wild male and female Atlantic salmon (*Salmo salar*) kelts retained in captivity for reconditioning and rematuration purposes respond to two 6-mo seasonally accelerated light cycles by spawning in the spring, 18–20 mo postspawning (Johnston et al. 1990). Accelerated 6-mo light cycles alter the normal cues such that gonadal maturation occurs when daylength is short and water temperature rising. These results demonstrate that accelerated light cycles can alter circannual endogenous reproductive cycles in Atlantic salmon and that oocyte development once initiated can be maintained by internal physiological conditions that are independent of external light cycles.

In other studies with domesticated female rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*), it has been demonstrated that gametogenesis can be accelerated and spawning advanced by 3 mo with compressed light cycles (Whitehead et al. 1978; Bromage et al. 1982a, 1982b; Duston and Bromage 1987, 1988). Time of first spawning in female trout can also be advanced with photoperiod manipulation (Bromage 1987).

Although photoperiod is an important regulator of oocyte development and spawning time, photoperiod does not act alone in controlling reproductive function. The extent to which temperature acts synergistically with photoperiod has been poorly described. Tyler et al. (1987) have shown that low temperature can reduce vitellogenin synthesis in the liver and vitellogenin uptake by oocytes in rainbow trout. Similar findings for Atlantic salmon have been reported by Johnston et al. (1987, 1990). Billard and Breton (1977), Manning and Kime (1985), and Beacham and Murray (1988) have also shown that the reproductive function of trout and west coast salmon is influenced by temperature. These findings suggest that it is likely that oocyte size and the time required for final egg maturation in Atlantic salmon may be governed by temperature. It is important, therefore, to describe the temperature conditions that produce large, good-quality eggs in Atlantic salmon. It is even more important to identify temperature conditions that favor egg production at different times of the year.

Knowledge of the role of temperature and photoperiod in controlling reproductive function may be helpful to aquaculturists and hatchery operators who are interested in producing 0+ smolts or in having salmon reproduce at times when conditions are more favorable for egg collection and early embryonic development. Any reduction in the time taken to produce smolts could provide considerable financial savings for the aquaculture industry. In addition, costs to the aquaculturists could be reduced if spring-spawning kelts could be spawned again in the spring of the next year. We therefore incorporated into this study an investigation to assess the effects of a time-shifted photoperiod on the timing of spawning by entrained spring-spawning kelts.

Recently, we demonstrated that Atlantic salmon kelts can be reconditioned and spawned in June following exposure to 6-mo compressed light cycles (Johnston et al. 1990). During that study, no attempt was made to measure the quality of gametes released in the spring or the level of egg and embryo survival. This study was designed to include these measurements together with an evaluation of the effect of varying winter water temperature on the time of spawning in the spring. The effect of temperature and photoperiod manipulation on kelt physiology was monitored through changes in body weight, condition factor and plasma calcium and alkaline phosphatase levels.

Materials and Methods

Facilities and Experimental Conditions

Early run salmon of Miramichi River stock were introduced in 1986 and 1987 into the Morell River, Prince Edward Island. During the summer of 1988, wild male and female Atlantic salmon of this stock were captured in a trap on the Morell River and transported to the Cardigan Salmonid Enhancement Centre where they were held until spawning and the commencement of this experiment.

The design of the experiment in the first year postspawning (January 1989 to December 1989) was to expose kelts to a natural temperature (NT) regime and two photoperiod conditions: natural photoperiod (NP) and two 6-mo compressed annual photocycles (2CP). In January 1990, kelts from these regimes that did not spawn in the fall of 1989 were then exposed to natural photoperiod and three different temperature regimes beginning in the spring of 1990. Fish that spawned in the spring of 1990 were then placed on a time-shifted photoperiod and a manipulated temperature regime to determine if spawning would occur again in the spring of 1991.

More specifically, on 14 January 1989, 16 female and 14 male postspawned grilse (fork length range = 49.5–57.0 cm) and 29 female and 2 male postspawned salmon (fork length range = 68.0–80.5 cm) were randomly divided between three 2.44-m-diameter center-draining fiberglass tanks (approximate water volumes of 2600 and 3400 L). Each tank received Cardigan River freshwater at approximately 38 L/min until 24 January 1990. During this period, water temperatures followed natural seasonal changes (Fig. 1).

Two different photoperiod regimes, NP and 2CP, similar to those described by Johnston et al. (1990), were used from January 1989 to December 1989. Kelts in two of the tanks received the 2CP regime, while those in the third tank received the NP regime. On 21 December 1989, 2CP tanks were placed on the NP regime until the end of the experiment.

On 22 January 1990, 36 kelts that had not spawned in the fall of 1989 were selected from the 2CP and NP regimes and placed in the three experimental temperature regimes. A total of five (2CP) females, three (2CP) males, three (NP) females, and one (NP) male were placed in each tank. The temperature conditions in each of the tanks were as follows. Tank 1 (NT regime) received Cardigan River water with water temperature following seasonal cycles until 31 May 1990; Tank 2 and Tank 3 were placed on well water having a constant temperature 7 ± 0.5°C. On 2 February, water temperature in Tank 2 (12–15°C regime) was increased to 12 ± 1.5°C until 24 April, increased to 15 ± 1°C until 30 April, and then decreased to 12 ± 1°C until June. Water temperatures in Tank 3 (7°C regime) remained constant at 7°C ± 0.5°C until June (Fig. 1).

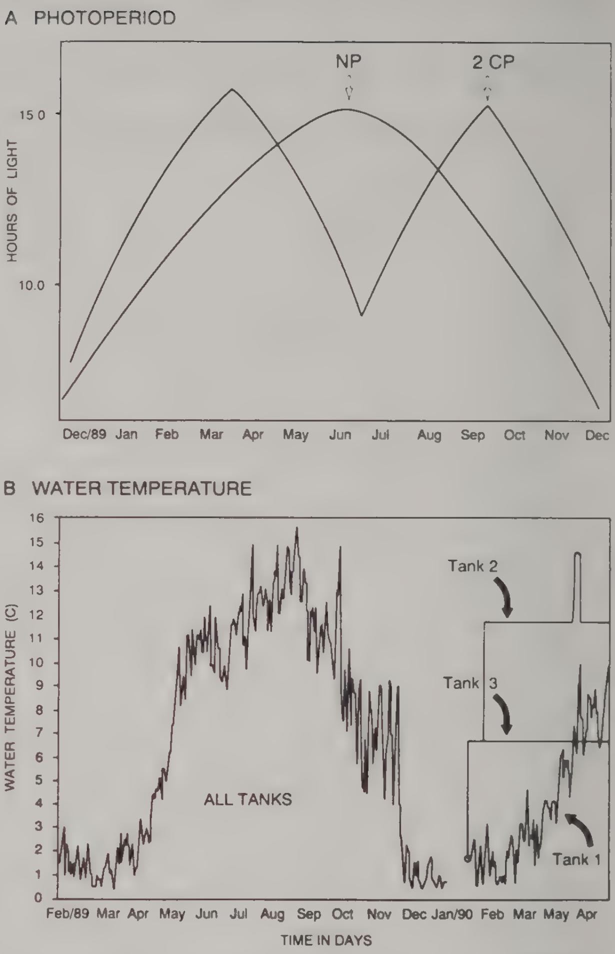

FIG. 1. Summary of natural (NP) and compressed 6-mo (2CP) light cycles and mean daily water temperatures supplied to each experimental regime between January 1989 and May 1991. Temperature conditions imposed in January 1990 are shown (Tank 1 = natural temperature (NT), Tank 2 = 12–15°C, Tank 3 = 7°C).

Water passing into each tank was degassed by falling over a vertical column of plastic rings. Each tank was covered with a screen to prevent salmon from jumping out. Each tank was illuminated with four 122-cm, 40-W General Electric cool white fluorescent light tubes placed approximately 122–183 cm above the tanks providing 247–516 lx of light at the water surface. Photoperiod conditions were the same for all tanks and daily photocycles were controlled by a timer that was manually set each week to simulate natural daylength for this region.

At the beginning of the experiment in 1989, grilse and salmon were anesthetised with tricaine methanesulphonate (MS 222; 100 mg/L), individually tagged, and initially force fed with a moist diet preparation. Once each day, a semimoist pellet (19 mm) prepared for broodstock by Connor Brothers, Blacks Harbour, New Brunswick, was offered. By April, only a few fish were feeding and it was necessary to offer in addition to the pellets freshly thawed smelts. This stimulated a more aggressive feeding response and by May, most fish were readily feeding.

Body measurements and blood samples were taken from each fish on 14 January, 6 June, 22 August, and 14 October 1989 and 13 January, 24 March, 30 April, 25 May, and 26 June 1990. Salmon were weighed (WT), measured for fork length (FL), and blood sampled from the caudal vessels. Plasma was harvested immediately and measured for alkaline phosphatase activity, calcium concentration, and osmolality in accordance with the procedures already described by Johnston et al. (1990).

At spawning, fecundity and egg diameters were determined in accordance with methods already described by Johnston et al. (1987). Semen was collected from each 2CP mature adult male salmon by abdominal massage. Sperm motility was evaluated by activating spermatozoa with 0.12 M NaCl and observing activity with a compound light microscope (40 ×). The volume of semen that was required to fertilize lots of 300 eggs with a ratio of 200 000 sperm/egg was determined according to Gallant (1990). Following egg fertilization, 300 eggs in each trial were placed in individually marked trays and checked daily for signs of egg mortality. All dead eggs were removed and recorded. A percentage survival to the eyed stage and to hatch was determined. Data sets were compared for statistical differences using Duncan's multiple range test or Student's *t*-test.

Repeat Spring Spawning of Entrained 2CP Females with Controlled Photoperiod and Temperature Manipulation

Following spawning in June 1990, four postspawned 2CP (7°C) and three postspawned 2CP (12–15°C) females together with several males were held at 7°C until 30 March 1991. On 30 March 1991 the water temperature was increased from 7 to 13°C until 22 April 1991. On 22 April 1991, water temperature was decreased to 7°C until the end of the experiment. All fish were held on simulated natural photoperiod until mid-August 1990 when a time-shifted photoperiod was implemented (Fig. 2). This photoperiod regime was designed to expose the entrained fish to a declining photoperiod, typical of that naturally experienced at spawning time in November, but time shifted to April 1991. Between April and the end of May fish were checked at different intervals to determine if they were ready for spawning.

Results

Reconditioning and Rematuration Responses

Between January and December 1989, reconditioning and rematuration responses varied with photocycle and age of the kelts. Although NP and 2CP grilse reached suitable body condition by October 1989, they did not spawn. However, of the salmon, two 2CP females (FL 73.2 and 79.5 cm; WT 4020 and 4460 g, respectively) in Tank 1 and two female salmon (FL 78.4 and 81.0 cm; WT 4600 and 5680 g, respectively) in Tank 2 matured and released eggs between 2 and 21 September 1989. One 2CP male (FL 64.2; WT 2770 g) in Tank 1 also matured by 2 September with motile spermatozoa, and another male matured with inactive spermatozoa on 21 September. Only these fish were stimulated by the accelerated photoperiod regime to spawn earlier than normal during that first year postspawning.

In the NP regime, two female salmon (FL 80.5 and 80.8 cm; WT 5120 and 5480 g, respectively) in Tank 3 matured and released eggs on 25 October 1989. Also, three NP males released milt by 14 October 1989; the remaining males did not show signs of spermiogenesis. None of the fish that spawned in the fall of 1989 were used in the temperature trials in 1990.

Compressed photocycles had little effect in stimulating female kelts to earlier or greater food consumption during 1989 when all groups received the same water temperatures. Initial mean weights of 2CP or NP kelts exposed to the three temperature regimes did not differ significantly in January 1989. Between June and August 1989, mean weight gains and condition factors (CF) increased for all groups (Fig. 3 and 4).

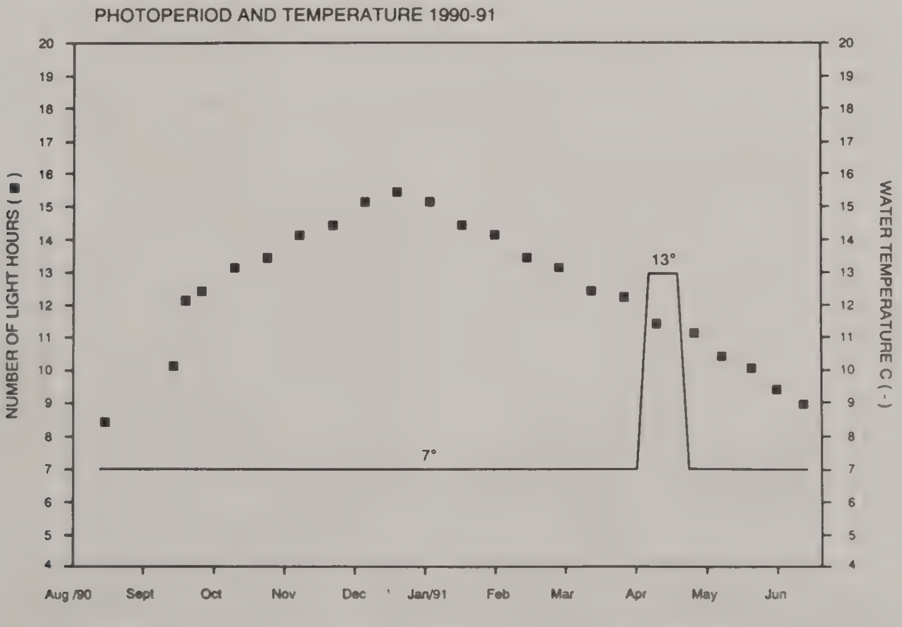

FIG. 2. Summary of the time-shifted photoperiod and temperature conditions used in 1990 and 1991 to recondition and remature kelts spawned in the spring of 1990.

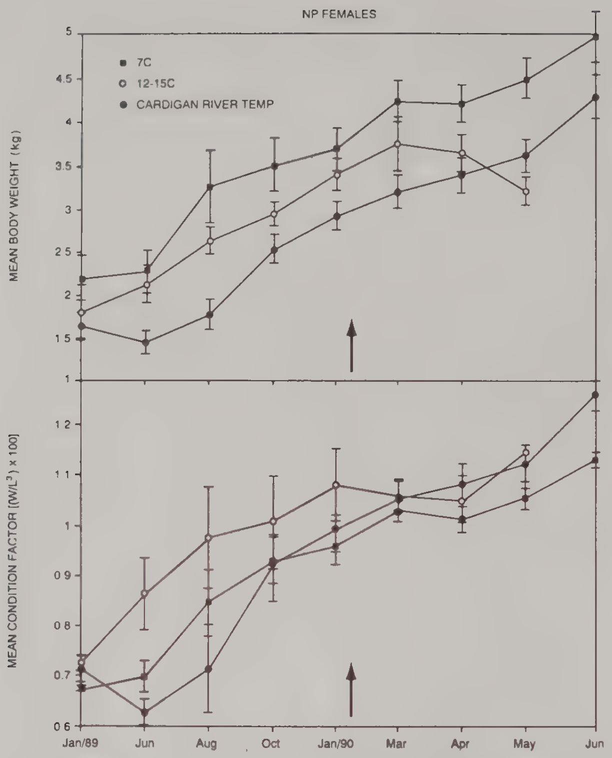

FIG. 3. Seasonal changes in the mean body weight and condition factor (± SE) of female kelts exposed to a simulated natural photoperiod (NP) and naturally fluctuating temperatures in 1989 and from 22 January 1990 (arrows) to three different temperature regimes (natural temperature (NT), 7°C, and 12–15°C) and NP.

Declining photoperiod in the first photocycle of the 2CP regime did not adversely affect weight gains. However, during the late fall of 1989 and early winter of 1990, weight gains declined as water temperature fell below 5°C.

Between January and June 1990, mean body weight and condition factor for female kelts in the NP regime changed with water temperature conditions (Fig. 3). Weight and condition factor for NP female kelts on Cardigan River water increased similar to those at 7°C. Although Cardigan River water temperatures were cold during the winter and spring of 1989 and 1990, kelts continued to feed and gain weight (Fig. 1). However, none of the kelts in the Cardigan River regime reached spawning condition by June 1990. Weight and condition factors for NP females at 12–15°C declined between March and June. This was due to the death of one kelt (FL 81.2 cm; WT 4470 g; CF 0.83) postsampling in April 1990. This particular kelt also lost weight between March and April. The cause of this weight loss and death is unknown but may be associated with the warmer water temperature, as a similar weight loss was observed for 2CP kelts on the same temperature regime.

Body weight and condition factor for 2CP females also varied with thermal regime (Fig. 4). Following exposure to 12°C in February, kelts in the 12–15°C regime reduced food intake and lost weight. When temperature was again increased to 15°C in early April, further weight losses occurred and there developed irregular pigmentation patches over the head and back of the fish. Loss of integumentary melanophores or failure in the mechanism that controls melanosome dispersion may have been responsible for the development of these whitish areas in the integument. Although weight losses and integumentary changes were evident, all females matured and were spawned out on 25 May 1990. Some of the weight losses in this group were associated with spawning. In the 7°C regime, weight and body condition of 2CP females declined from April to June as females matured and spawned. Three 2CP females at 7°C matured and released eggs in late March, while another was spawned out on 25 May 1990. The remaining female in this regime had a low condition factor (0.87) in January 1990 and did not mature by June 1990. Female kelts on Cardigan River water gained weight and body condition and failed to spawn in the spring.

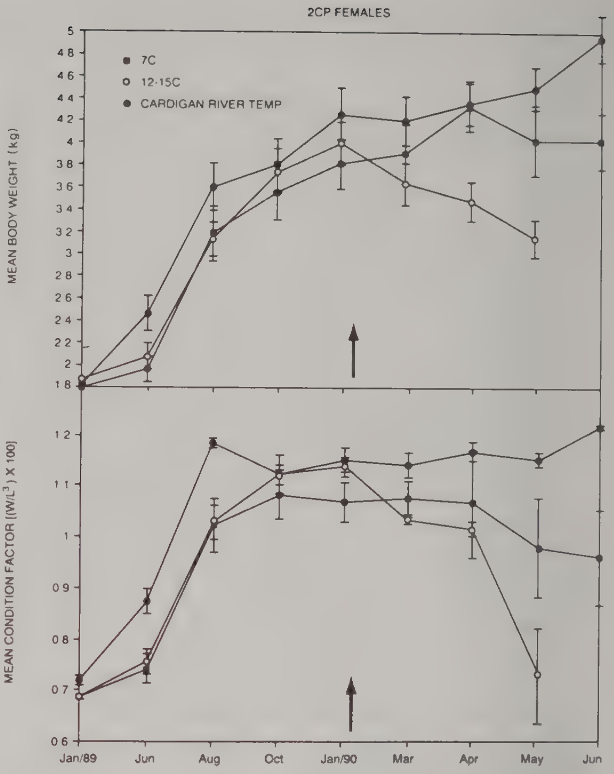

FIG. 4. Seasonal changes in the mean body weight and condition factor (± SE) for female kelts exposed to two 6-mo compressed photoperiod cycles (2CP) and naturally fluctuating temperatures in 1989 and from 22 January 1990 (arrows) to three different temperature regimes (natural temperature (NT), 7°C, and 12–15°C) and a simulated natural photoperiod (NP).

Males from 2CP exposed to the 12–15°C regime were also adversely affected by high spring temperatures and lost weight and condition factor. Like the females, all of the males matured and were running milt by May 1990. All fish that spawned had condition factors over 1.09 in the spring of 1990. None of the 2CP males at 7°C released sperm in the spring even though females were mature in the same tank. None of the NP males in the 7°C or Cardigan River regimes matured.

Blood Calcium and Alkaline Phosphatase Levels

Plasma calcium concentrations and alkaline phosphatase activity increased significantly ($p < 0.05$) in both groups prior to egg release, with peaks in March and April (Fig. 5 and 6). Females placed in Cardigan river water at lower water temperatures in the winter did not mature or have significantly elevated

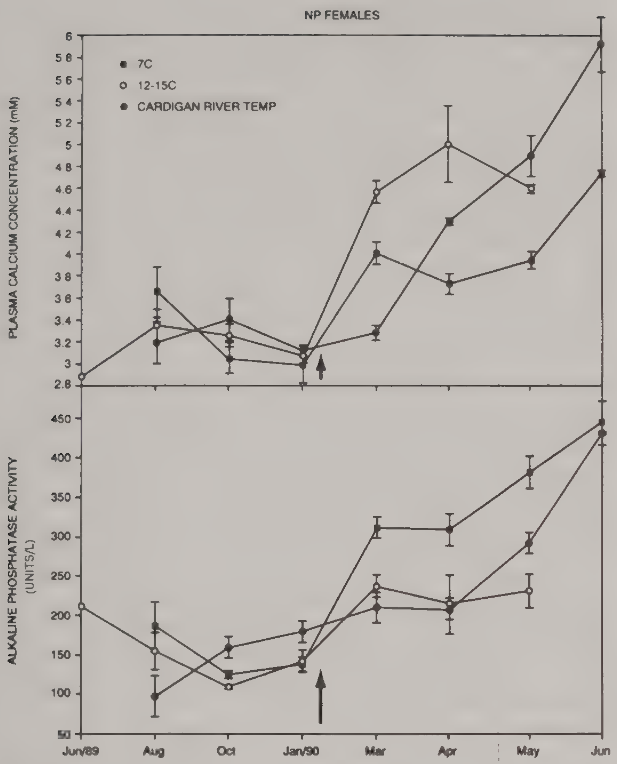

FIG. 5. Seasonal changes in the mean plasma calcium concentration and alkaline phosphatase activity (± SE) for female kelts exposed to a simulated natural photoperiod (NP) and naturally fluctuating temperature in 1989 and from 22 January 1990 (arrows) to three different temperature regimes (natural temperature (NT), 7°C, and 12–15°C) and NP. Calcium and alkaline phosphatase levels in 1989 are for kelts used in the three temperature regimes in 1990.

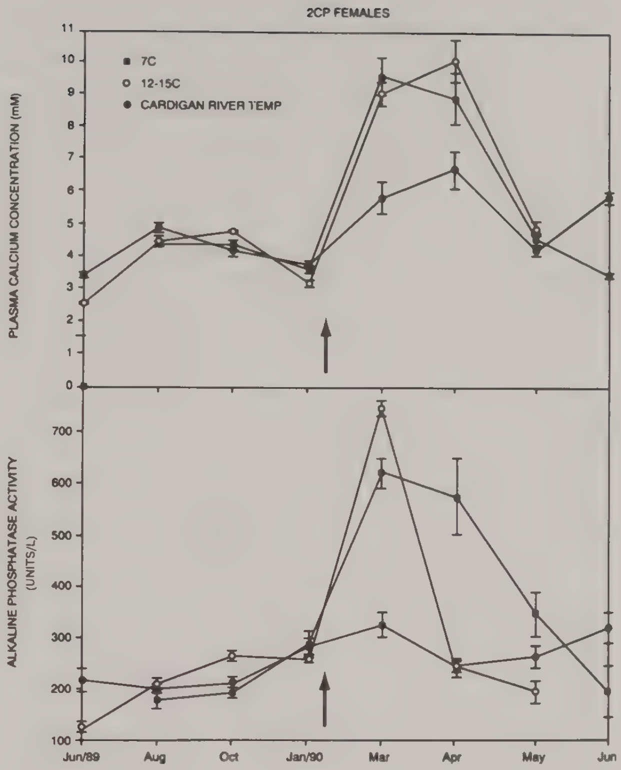

FIG. 6. Seasonal changes in the mean plasma calcium concentration and alkaline phosphatase activity (± SE) for female kelts exposed to two 6-mo compressed light cycles (2CP) and naturally fluctuating temperatures in 1989 and from 22 January 1990 (arrows) to three different temperature regimes (natural temperature (NT), 7°C, and 12–15°C) and a simulated natural photoperiod (NP). Calcium and alkaline phosphatase levels in 1989 are for kelts used in the three temperature regimes in 1990.

plasma levels. The exposure of 2CP females to high water temperature in the spring caused a marked and significant reduction in alkaline phosphatase activity by April whereas fish at 7°C had a more gradual reduction in activity. Regardless of temperature regime, NP females did not mature in the fall of 1989 or the spring of 1990, but they did show some marginally significant ($p < 0.07$) elevation in calcium levels between January and June 1990. Significant elevations ($p < 0.05$) in alkaline phosphatase activity also occurred by June 1990 for all NP groups. During the summer of 1990, NP females continued to mature and were spawned out between 17 and 23 October 1990. Elevations in calcium and alkaline phosphatase activity in June 1990 were associated with increased food consumption and oocyte growth and development.

Alkaline phosphatase activity and plasma calcium concentrations in males fluctuated slightly with season and regime, but there were no significant differences between groups or at different sampling times except for 2CP males in Cardigan river water between April and June 1990. Plasma calcium and alkaline phosphatase activity levels for males ranged between 2.5 and 4.1 mM and 70 and 200 units/L, respectively.

Plasma osmolalities for males and females in each regime ranged between 318 and 365 mosmol/kg, with most values falling between 330 and 350 mosmol/kg. There were no significant differences between mean plasma osmolalities for each sex in the different photoperiod and temperature regimes or at the different sampling times.

Success of Spring-Spawned Eggs Fertilized with Fresh Sperm

The mean number of eggs per centimetre fork length (± standard error) for spring spawners in the 2CP regimes was 65.1 (±9.91). This was not significantly different from the mean number of eggs per centimetre fork length of 81.1 (±10.9) for salmon spawned in the fall in an earlier study (Johnston et al. 1987). The mean egg size (± standard error) for spring-spawned salmon was 0.509 (±1.06) cm. This was significantly smaller ($p < 0.001$) than the mean egg size of 0.592 (±1.23) cm for the 1987 study. Egg survival to the eyed stage following fertilization with fresh sperm ranged between 44.3 and 73.0% and to the hatch stage between 38.7 and 62.2%. Although these values are lower than similar data collected for fall-spawned fish, they do demonstrate that spring-spawned eggs fertilized with fresh sperm are viable and produce robust embryos that will hatch normally.

Repeat Spring Spawning of 2CP Females

Following spawning in June 1990, four postspawned 2CP (7°C) and three postspawned 2CP (12–15°C) females together with several males were held in experimental conditions until

May 1991 to determine if they would spawn in the spring of 1991. Females were checked for maturation on 17 April 1991 and one female from the initial 2CP (7°C) had released eggs and was overripe. This female probably matured in mid-March 1991. Another female from the initial 2CP (12–15°C) was ripe and spawned 5184 eggs with an egg diameter of 4.8 mm. On 29 April, a female from 2CP (12–15°C) died from fungus infection; a postmortem examination indicated that the oocytes were maturing and near full size for spawning. On 20 May, another female from the initial 2CP (7°C) was spawned with egg diameters of 5.5 mm. None of the other females in this photoperiod and temperature regime matured. In summary, of the 2CP (7°C) females, two of four spring spawners of 1990 spawned in June 1991, while of the 2CP (12–15°C) females, two of three spawned in the spring of 1991.

Discussion

The present study confirms earlier findings of Johnston et al. (1990) that the timing of reproductive maturation of Atlantic salmon kelts can be altered with the use of two 6-mo compressed photocycles and that entrained kelts will mature and release eggs in the spring. It also demonstrates that in the first year in captivity, a few larger salmon with sufficient body condition will respond to the 2CP photocycle and spawn several months earlier than normal, while other kelts remain refractory.

It is evident that temperature is an important factor in controlling gonadal development. Water temperatures from 0 to 4°C during the winter arrested gonadal growth in both male and female kelts. Failure of oocyte development, as evidenced by plasma calcium and alkaline phosphatase levels, suggests that hepatocytes in the liver decreased vitellogenin synthesis and release. It is probable that temperature suppressed the synthesis and release of hormones from the hypothalamic–pituitary complex, thereby governing the production of estradiol from the ovary and subsequent synthesis of vitellogenin in the liver and more directly lowered the level of cellular metabolism in the liver. Cold-water conditions also suppressed the reproductive function of 2CP males, for not a single kelt matured to release sperm. Clearly, low temperature conditions can override the physiological responses initiated by photoperiod by slowing down or completely arresting gamete development until more favorable thermal conditions prevail.

Elevation of water temperature to 15°C in the spring also had an adverse effect on kelts by increasing the time taken for oocytes to mature. This response was most probably associated with a thermally stimulated cortisol suppression of reproductive endocrinology (Billard et al. 1981; Pickering 1989). In the wild, it is not unusual for Atlantic salmon to encounter summer water temperatures of 15°C or more during upstream spawning migrations and normally, such temperatures have little effect on the functions of the fish. Warmwater temperatures in the summer probably facilitate exogenous vitellogenesis and increase oocyte size and number. It was for this reason that a 15°C increase was imposed in the spring in this experiment. However, such a temperature increase in the spring created a severe and acute stress which altered kelt behavioral and physiological responses. Kelts appeared to tolerate 12°C without any adverse effects; therefore, we conclude that this temperature would be more appropriate for stimulating reproductive function. Kelts maintained at 12°C would probably mature and release eggs or sperm earlier in the spring than was demonstrated in this study.

The level of reconditioning that kelts attain prior to vitellogenesis influences the rematuration process. Kelts of either sex with high condition factors generally initiate gonadal development more frequently than those with low condition (Johnston et al. 1990; Crim et al. 1992). Kelts with low fat or protein reserves seem less responsive to photoperiod and temperature manipulation and/or rematuration signals. Anorexic males or females with low condition factors have low plasma T_3 and T_4 levels (Eales et al. 1991); reconditioning may be influenced by the failure of the hypothalamus or pituitary to release TSH-RH or TSH, respectively, to stimulate the thyroid follicles in the spring. While the correct combination of photoperiod and temperature signals is needed for reconditioning and rematuration, other factors such as the genetic background of the stock, stress in captivity, nutrition, and other endocrine interactions may also influence reproductive responses.

While it is possible to manipulate the reproductive function of kelts to produce eggs and sperm at different times of the year, often one sex may ripen in advance of the other. Maintaining both sexes together in the same tank helps to assure that gamete maturation will occur at the same time. Pheromone and behavioral cues appear to assist in gonadal development and final maturation of both male and female fish (Van den Hurk and Resink 1992). Some male kelts, however, may not respond to environmental or pheromonal cues and an alternative source of sperm for egg fertilization may be needed. Cryopreserved spermatozoa from males spawned in the fall may be suitable as an alternative. Further research is needed into the development of reliable techniques for the preservation of Atlantic salmon gametes so that alternatives will be available to hatchery managers.

The present results demonstrate that it is possible to interrupt the natural endogenous reproductive cycle of male and female Atlantic salmon kelts and entrain them with controlled photoperiod and temperature conditions to reproduce at times other than October and November. It is also possible to maintain an altered spawning time by time shifting the environmental cues. These results support the view that the primary control mechanism for spring spawning occurs through photoperiodic entrainment of the reproductive cycle with temperature and body condition acting as a modifier and rate-determining factor. Only when temperature is outside the thermal range for normal tissue function will there be a reduced rate of gonadal development and a radically modified time of maturation.

The development of techniques for spawning kelts at different times in the year offers both practical and economic advantages to the aquaculture industry. Such benefits would include the establishment of year-round hatchery production rather than that limited to the short spawning seasons in the fall. As well, gamete collection could occur when weather and water conditions are more favorable. Eggs fertilized in the spring could develop immediately and hatch when water temperatures are higher, favoring more rapid early growth. This would avoid overwinter egg losses due to harsh environmental conditions and/or disease. Early rapid growth may have significant impacts for greater production in a shorter time period. With the correct timing of egg release and hatch, combined with forced early rapid growth, it may be possible to produce a 0+ smolt for ocean culture in the spring or fall. Reduction in the age to smolting by 1 yr could give hatcheries and the aquaculture industry considerable financial benefits.

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Corynosoma wegeneri (Acanthocephala: Polymorphida) and *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) Larvae in Scotian Shelf Groundfish

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Marcogliese, D. J., and G. McClelland. 1992. *Corynosoma wegeneri* (Acanthocephala: Polymorphida) and *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) larvae in Scotian Shelf groundfish. Can. J. Fish. Aquat. Sci. 49: 2062–2069.

We examined larvae of the seal parasites *Corynosoma wegeneri* and *Pseudoterranova decipiens* in various fish species collected from Western and Sable Island banks between February 1989 and October 1990. Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), American plaice (*Hippoglossoides platessoides*), yellowtail flounder (*Pleuronectes ferrugineus*), windowpane (*Scophthalmus aquosus*), longhorn sculpin (*Myoxocephalus octodecemspinosus*), and sea raven (*Hemitripterus americanus*) were infected by both parasites, longhorn sculpin being a new host record for *C. wegeneri*. Only *C. wegeneri* occurred in winter flounder (*Pleuronectes americanus*), and neither parasite was found in northern sand lance (*Ammodytes dubius*) or capelin (*Mallotus villosus*). The two parasites were most numerous in sea raven and longhorn sculpin. *Corynosoma wegeneri* was more prevalent in fish sampled in 1989–90 than in previous surveys of Atlantic cod and haddock from the Scotian Shelf. *Pseudoterranova decipiens* and *C. wegeneri* occurred throughout the sampling area, but small fishes in the vicinity of Sable Island had the heaviest sealworm infections, and both parasites in longhorn sculpin declined with distance from Sable Island. Increases of *C. wegeneri* in groundfish, like recent increased levels of *P. decipiens* infection on the Scotian Shelf, can be attributed to the dramatic growth of the grey seal (*Halichoerus grypus*) population on Sable Island.

Nous avons examiné les larves des parasites du phoque *Corynosoma wegeneri* et *Pseudoterranova decipiens* chez diverses espèces de poissons capturés sur le banc Western et le banc de l'île de Sable entre février 1989 et octobre 1990. La morue franche (*Gadus morhua*), l'aiglefin (*Melanogrammus aeglefinus*), la plie canadienne (*Hippoglossoides platessoides*), la limande à queue jaune (*Pleuronectes ferrugineus*), le turbot de sable (*Scophthalmus aquosus*), le chaboisseau à dix-huit épines (*Myoxocephalus octodecemspinosus*) et l'hémitriptère atlantique (*Hemitripterus americanus*) étaient infectés par les deux parasites, mais c'était la première fois qu'on observait *C. wegeneri* chez le chaboisseau à dix-huit épines. Seul ce dernier parasite se retrouvait chez la plie rouge (*Pleuronectes americanus*), et on n'en a trouvé aucun chez le lançon (*Ammodytes dubius*) ni chez le capelan (*Mallotus villosus*). Les deux parasites présentaient les effectifs les plus élevés chez l'hémitriptère atlantique et le chaboisseau à dix-huit épines. *Corynosoma wegeneri* était plus fréquent chez les poissons échantillonnés en 1989–1990 que chez les poissons capturés lors de relevés précédents portant sur la morue franche et l'aiglefin du plateau de Nouvelle-Écosse. *Pseudoterranova decipiens* et *C. wegeneri* étaient présents dans toute la zone d'échantillonnage, mais les poissons de petite taille se trouvant à proximité de l'île de Sable présentaient les infestations les plus fortes par le ver du phoque, et la présence des parasites chez le chaboisseau à dix-huit épines décroissait à mesure qu'augmentait la distance par rapport à l'île de Sable. On peut attribuer l'augmentation du nombre de *C. wegeneri* chez le poisson de fond, tout comme l'accroissement récent de l'infestation des poissons du plateau de Nouvelle-Écosse par *P. decipiens*, à l'augmentation spectaculaire de la population de phoques gris (*Halichoerus grypus*) sur l'île de Sable.

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Recent studies have reported significant increases in the levels of larval sealworm (*Pseudoterranova decipiens*) infection in groundfish in the Northwest Atlantic, particularly in Scotian Shelf populations (McClelland et al. 1983b, 1987, 1990). This nematode has been reported from 44 species of fish from the Northwest Atlantic (McClelland et al. 1990), and the grey seal (*Halichoerus grypus*), among other phocids, appears to be the most important definitive host (McClelland et al. 1983a). The largest concentration of grey seals in eastern Canadian waters occurs on Sable Island, 290 km east of Halifax, Nova Scotia. Pup production on the island has increased 20-fold between 1962 and 1988 (Zwanenburg and Bowen 1990). Noting that levels of larval sealworm infection in groundfish increase with proximity to seal colonies (Scott and Martin 1957; McClelland et al. 1983b), investigators have speculated that levels of sealworm infection in fish are related primarily to grey seal population densities (Young 1972; McClelland et al. 1985; McClelland 1990).

Grey seals are definitive hosts for a second parasite, the acanthocephalan *Corynosoma wegeneri* (Montreuil 1958), which uses fish as paratenic hosts. Larval stages (cystacanths) of *Corynsoma* spp. are reported from 12 fish species in the Northwest Atlantic (Bullock 1958; Margolis and Arthur 1979; Appy and Burt 1982; Scott 1987). Levels of infection are usually low (Ronald 1963; Scott 1981, 1985, 1987; Scott and Bray 1989), the highest number per individual host (11) being reported in Atlantic cod (*Gadus morhua*) (Appy and Burt 1982). In a preliminary survey, various species of groundfish collected on the Scotian Shelf during February 1989 were examined at sea for *C. wegeneri*. Cystacanths were remarkably numerous in the few fish examined; for example, >200 were found in an individual sea raven (*Hemitripterus americanus*).

To investigate the possibility of concurrent increases in levels of larval *C. wegeneri* and *P. decipiens* infection in fishes from the Scotian Shelf as a consequence of the growth of the grey seal population, the two helminths were surveyed in 10 species of fish in February and May 1990. As both *C. wegeneri* and *P. decipiens* may use amphipods as intermediate hosts (Petrochenko 1956; McClelland 1990), we tested for positive associations of these helminths in fish hosts and for differences in mean counts of the two parasite species in the shared hosts. We also tested correlations of infection levels of both parasites in fish from Sable Island – Western Bank complex with distance from Sable Island, the focal point of the grey seal population on the Scotian Shelf. Results presented herein demonstrate that levels of *C. wegeneri* infection in groundfish from the Scotian Shelf have increased considerably since previous surveys were conducted and that levels of infection of both parasites in fish tend to increase with proximity to Sable Island.

Materials and Methods

Samples were collected using otter trawls deployed from the RV *Alfred Needler* in February 1989 and 1990, the RV *Lady Hammond* in June 1989 and October 1990, and the RV *E. E. Prince* in May 1990. Samples collected are listed by fish species in Table 1, and the sampling sites are indicated in Fig. 1. All fish were bagged, labelled, frozen, and returned to the laboratory for subsequent examination. Fish were thawed, measured, and weighed and the viscera were removed and examined for *P. decipiens*. Fillets and napes were thin-sliced and inspected for sealworm with the unaided eye. This method has been shown to be accurate and reliable (McClelland et al. 1983a). Viscera of fish collected in February and May 1990 were also examined for *C. wegeneri*. To confirm identification, probosces of worms were everted by applying pressure to the body in the region of the proboscis receptacle with a blunt instrument and identified according to Arai (1989). Fish examined for sealworm only and for both sealworm and *C. wegeneri* are listed in Table 1. Pearson product-moment correlation coefficients between mean parasite counts and host size, parasite counts and distance from Sable Island, and counts of *P. decipiens* and *C. wegeneri* in the same hosts were calculated using the Statistical Analysis System (SAS Institute, Inc. 1988). Parasite counts were $\log_{10}(n + 1)$ transformed before performing these analyses. For comparison of mean sealworm counts in fishes collected ≤20 and 50–60 km from Sable Island, fish were divided into 5-cm length strata (≤15, 16–20. . ., 41–45, ≥46), and *t*-tests were employed for samples with equal variances and, where appropriate, for samples with unequal variances. Differences between mean counts of each helminth in shared fish hosts were tested with *t*-tests for samples with equal variances and, where appropriate, for samples with unequal variances. Similarly, *t*-tests for samples with unequal variances were employed for comparisons of *C. wegeneri* counts in different length groups of yellowtail and winter flounder (yellowtail flounder (*Pleuronectes ferrugineus*, previously *Limanda ferruginea*) and winter flounder (*Pleuronectes americanus*, previously *Pseudopleuronectes americanus*)). ANOVA was used to compare mean transformed ($\log_{10}(n + 1)$) sealworm counts in each length group of yellowtail flounder from three sites, 3.5, 39, and 50 km from Sable Island. Probability values <0.05 were defined as significant.

TABLE 1. Sampling regime, including species of fish, date of collection, site of capture, and number of fish, for fish examined for *P. decipiens* only (P) and for both *P. decipiens* and *C. wegeneri* (CP). Sites of capture correspond to sampling sites on Fig. 1.

Species	Date (mo/yr)	Site	*n*	Parasites
Mallotus villosus	5/90	1	2	CP
(capelin)	5/90	2	51	CP
Gadus morhua	5/90	1	3	CP
(Atlantic cod)	5/90	2	2	CP
	5/90	3	21	CP
	5/90	4	1	CP
Melanogrammus aeglefinus	5/90	1	1	CP
(haddock)	5/90	3	20	CP
	5/90	4	19	CP
	5/90	5	20	CP
Ammodytes dubius (northern sand lance)	5/90	2	60	CP
Hemitripterus americanus	2/89	1	38	P
(sea raven)	2/89	2	102	P
	2/90	7	4	CP
	5/90	1	3	CP
	5/90	4	7	CP
Myoxocephalus	2/89	1	54	P
octodecemspinosus	2/89	2	101	P
(longhorn sculpin)	5/90	1	18	CP
	5/90	2	30	CP
	5/90	3	18	CP
	5/90	4	10	CP
	5/90	5	3	CP
Scophthalmus aquosus (windowpane)	5/90	3	10	CP
Hippoglossoides platessoides	2/89	1	300	P
(American plaice)	2/89	2	186	P
	2/90	1	40	CP
	5/90	1	5	CP
	5/90	2	1	CP
	5/90	4	2	CP
	5/90	5	11	CP
Pleuronectes ferrugineus	2/89	2	162	P
(yellowtail flounder)	6/89	2	138	P
	2/90	1	3	CP
	2/90	7	26	CP
	5/90	1	7	CP
	5/90	2	32	CP
	5/90	3	37	CP
	5/90	4	32	CP
	5/90	5	32	CP
	10/90	6	109	P
Pleuronectes americanus	5/90	1	15	CP
(winter flounder)	5/90	2	15	CP
	5/90	3	42	CP
	5/90	4	37	CP

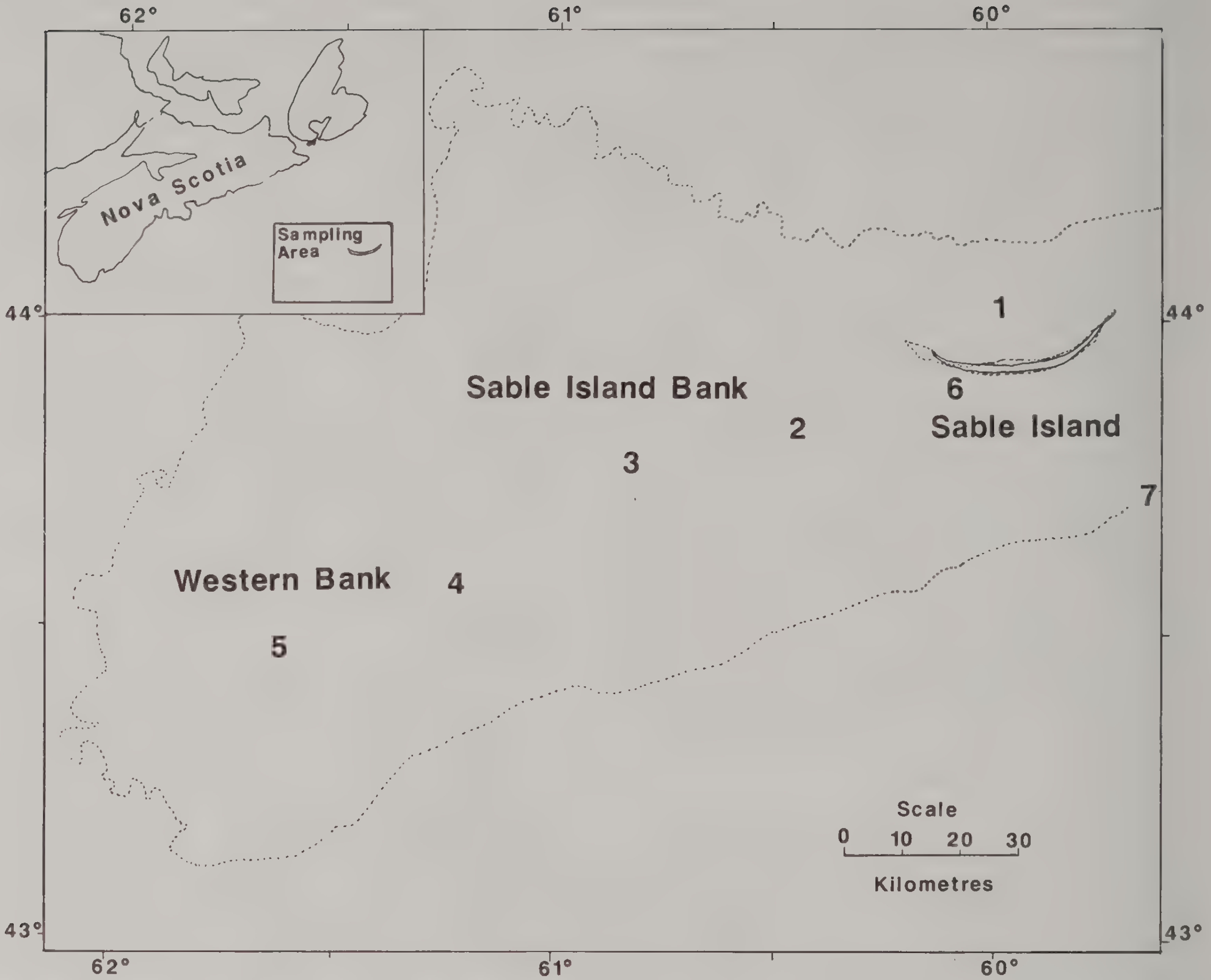

FIG. 1. Map of Sable Island and Western banks, Sable Island, and sampling locations. Numbers of sampling locations correspond to those in Table 1. Inset: location of sampling area relative to eastern Canada.

The terms prevalence, abundance, and intensity are used in accordance with Margolis et al. (1982). Prevalence refers to the percentage of infected hosts in a sample, abundance the mean number of parasites per host, and intensity the number of parasites in an individual host.

Results

Corynosoma wegeneri was found in eight of the 10 species of fish collected from the Sable Island – Western Bank area in February and May 1990; only northern sand lance (*Ammodytes dubius*) ($n = 60$) and capelin (*Mallotus villosus*) ($n = 53$) were not infected (Table 2). Sea raven and longhorn sculpin (*Myoxocephalus octodecemspinosus*), with prevalences of 100 and 97.3% respectively, were the most heavily infected (Table 2). Abundances in these two species were approximately an order of magnitude greater than those found in other fish; the maximum abundance was 49.71 in sea raven. In other hosts sampled, prevalences of *C. wegeneri* ranged from 33.3% in haddock (*Melanogrammus aeglefinus*) to 64.5% in yellowtail flounder, with abundances varying from 0.72 in winter flounder to 4.85 in Atlantic cod (Table 2). Abundance of *C. wegeneri* increased significantly with host length in yellowtail flounder ($p \leq 0.0001$), winter flounder ($p < 0.003$), longhorn sculpin ($p \leq 0.0001$), and sea raven ($p < 0.0005$). Among the flatfish, abundance and prevalence of *C. wegeneri* were significantly ($p < 0.01$) higher in yellowtail flounder than in winter flounder for all size classes of fish except those ≤20 cm (Fig. 2).

Sealworm was found in all fish species examined except capelin, northern sand lance, and winter flounder. Levels of larval *P. decipiens* infection were greatest in sea raven, longhorn sculpin, American plaice (*Hippoglossoides platessoides*), and windowpane (*Scophthalmus aquosus*), with abundance and prevalence ranging from 3.40 to 63.29 and 70 to 100%, respectively (Table 2). In other fishes, prevalence and abundance ranged from 11.7% and 0.17 in haddock to 48.2% and 1.22 in Atlantic cod (Table 2). There were significant positive correlations between sealworm abundance and host length in longhorn sculpin ($p \leq 0.0001$), sea raven ($p \leq 0.0001$), yellowtail flounder ($p \leq 0.0001$), and American plaice ($p \leq 0.0001$).

While there was a significant positive correlation between the abundances of *P. decipiens* and *C. wegeneri* in longhorn

TABLE 2. Prevalence (*P*), abundance (*A*), standard error (SE), and intensity (*I*) of *C. wegeneri* and *P. decipiens* in fishes caught on Western and Sable Island banks in February and May 1990.

Host	*n*	*C. wegeneri*			*P. decipiens*		
		P (%)	*A* ± SE	*I* range	*P* (%)	*A* ± SE	*I* range
Gadus morhua (Atlantic cod)	27	59.3	4.85 ± 6.69	1–24	48.2	1.22 ± 2.14	1–8
Melanogrammus aeglefinus (haddock)	60	33.3	1.17 ± 2.34	1–12	11.7	0.17 ± 0.49	1–2
Hemitripterus americanus (sea raven)	14	100	49.71 ± 56.94	6–168	100	63.29 ± 45.32	10–178
Myoxocephalus octodecemspinosus (longhorn sculpin)	109	97.3	18.42 ± 19.76	1–103	87.2	6.46 ± 8.48	1–63
Scophthalmus aquosus (windowpane)	10	50.0	1.50 ± 2.07	1–6	70.0	3.40 ± 2.84	1–7
Hippoglossoides platessoides (American plaice)	59	35.6	0.73 ± 1.41	1–8	81.4	5.24 ± 7.87	1–50
Pleuronectes ferrugineus (yellowtail flounder)	169	64.5	2.66 ± 3.75	1–29	29.0	0.47 ± 0.96	1–7
Pleuronectes americanus (winter flounder)	109	45.3	0.72 ± 1.60	1–10	0.0	0.00	—

sculpin ($p < 0.005$), relationships between the abundances of the two parasite species in other fish hosts were not evident. However, *C. wegeneri* outnumbered *P. decipiens* in longhorn sculpin ($p \leq 0.0001$), yellowtail flounder ($p \leq 0.0001$), winter flounder ($p \leq 0.0001$), Atlantic cod ($p \leq 0.05$), and haddock ($p \leq 0.005$). *Pseudoterranova decipiens* were more abundant than *C. wegeneri* in American plaice ($p \leq 0.0001$). Differences in abundances of the two parasites were not significant in windowpane.

Prevalences of *C. wegeneri* and *P. decipiens* were high in groundfish samples taken along a transect across Western and Sable Island banks, but abundances of both helminths were negatively correlated with distance from Sable Island in longhorn sculpin ($p < 0.01$ for *C. wegeneri*, $p \leq 0.0001$ for sealworm). Similarly, abundances in yellowtail flounder also declined with distance from Sable Island ($p < 0.05$ for sealworm, $p > 0.05$ for *C. wegeneri*) (Fig. 3 and 4).

Sealworm abundances in fishes taken <20 km from Sable Island were higher than those occurring in the same species collected 50–60 km from the island; according to *t*-tests the disparities in worm abundance were significant in longhorn sculpin 16–30 cm ($p < 0.05$), sea raven ≤30 cm ($p < 0.05$), and American plaice ≤30 cm ($p \leq 0.0001$) (Table 3). In contrast, sealworm were more numerous ($p < 0.05$) in 26- to 35-cm American plaice collected 50–60 km from Sable Island than in those taken <20 km from the island. Sealworm abundances in yellowtail flounder collected 3.5 km south of the island, 39 km southeast of the island, and 50–60 km southwest of the island did not vary significantly (ANOVA, $p > 0.2$).

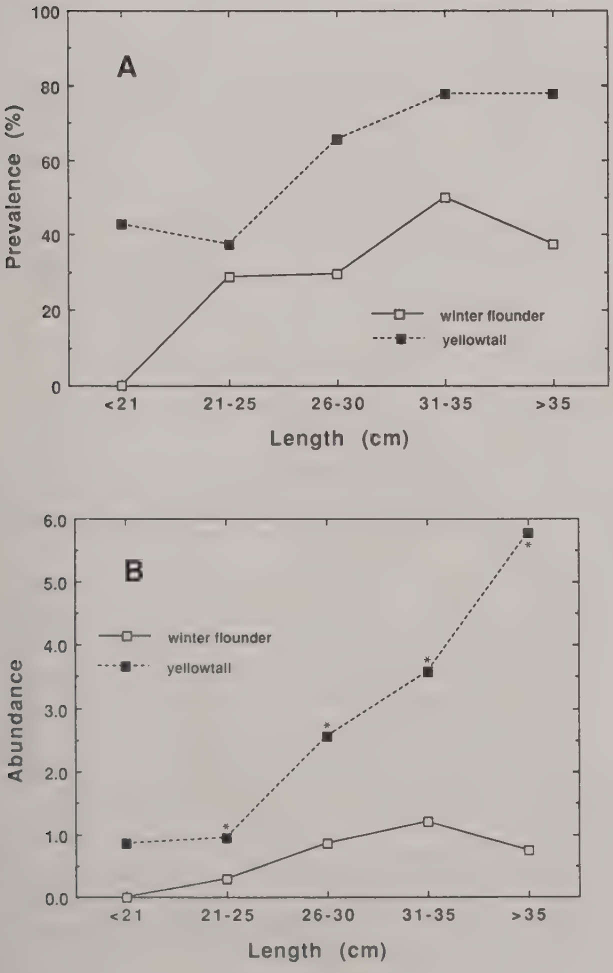

FIG. 2. (A) Prevalence and (B) abundance of *C. wegeneri* in various size classes of yellowtail and winter flounder collected on Western and Sable Island banks during February and May 1990. Abundance values that are significantly different between the two host species are indicated by an asterisk.

TABLE 3. Prevalence (*P*), abundance (*A*), standard error (SE), and intensity (*I*) of *P. decipiens* in fishes taken ⩽20 km to the north (site 1) and 50–60 km southwest (site 3) of Sable Island in 1989 and 1990. Abundances at site 1 and site 3 significantly different at $*p < 0.05$, $**p < 0.005$, and $***p < 0.0005$.

		Site 1				Site 3			
Species	Length (cm)	*n*	*P* (%)	*A* ± SE	*I* range	*n*	*P* (%)	*A* ± SE	*I* range
Hemitripterus americanus (sea raven)	⩽20	14	92.9	21.64 ± 14.28	6–52	10	80.0	5.70 ± 5.50	1–14**
	21–25	7	100	33.14 ± 15.31	2–47	18	100	14.94 ± 8.67	1–35***
	26–30	13	100	94.31 ± 61.88	17–277	23	100	44.83 ± 33.36	4–162*
	31–35	10	100	80.20 ± 38.28	19–138	18	100	57.22 ± 21.99	17–112
	36–40	0				20	100	111.60 ± 81.77	10–289
	41–45	1	100	254	254	10	100	130.10 ± 68.91	58–276
	⩾46	0				3	100	222.00 ± 100.64	58–338
Myoxocephalus octodecemspinosus (longhorn sculpin)	⩽15	33	78.8	6.00 ± 7.28	1–26	2	100	1.50 ± 0.71	1–2
	16–20	10	90.0	7.50 ± 8.05	6–25	10	80.0	1.40 ± 1.26	1–4*
	21–25	32	100	16.78 ± 12.82	2–63	42	85.7	4.12 ± 5.26	1–31***
	26–30	25	100	18.20 ± 15.96	1–59	60	98.3	7.15 ± 5.98	1–31**
	31–35	2	100	6.50 ± 7.78	1–12	17	94.1	12.47 ± 16.80	1–62
Hippoglossoides platessoides (American plaice)	⩽15	72	75.0	4.49 ± 7.60	1–50	35	14.3	0.17 ± 0.45	1–2***
	16–20	67	92.5	10.55 ± 9.63	1–42	56	50.0	0.93 ± 1.36	1–8***
	21–25	32	93.8	11.66 ± 13.26	1–61	63	95.2	8.52 ± 10.26	1–58
	26–30	33	90.9	9.48 ± 10.98	1–17	68	97.1	15.10 ± 10.91	1–51*
	31–35	106	96.2	11.02 ± 12.67	1–76	87	100	17.84 ± 14.89	1–82**
	36–40	34	97.1	14.32 ± 26.50	1–114	39	100	14.51 ± 10.66	1–39
	⩾41	1	100	1.00	1	15	100	12.33 ± 15.98	1–48

Discussion

Levels of *C. wegeneri* infection in groundfish from the Scotian Shelf in 1990 were generally higher than those previously reported. Prevalence of the parasite in Atlantic cod from the Sable Island area was 59.3% in 1990, while Appy and Burt (1982) reported that the overall prevalence of *Corynosoma* sp. was only 14.2% in Atlantic cod from the Scotian Shelf and the southern Gulf of St. Lawrence. In Scotian Shelf haddock, prevalence of *Corynosoma* sp. was 1.1% according to Scott (1981), but 33.3% in the present study. Earlier studies also report extremely low prevalences in pollock (*Pollachius virens*) (0.43%) (Scott 1985) and in red (*Urophycis chuss*) (2%) and white hake (*U. tenuis*) (3%) from the Scotian Shelf (Scott 1987), although these latter species were not surveyed in the present study. There is no prior record of *C. wegeneri* from sea raven in Canadian waters, nor has this parasite been reported from longhorn sculpin.

Abundances and prevalences of *P. decipiens* in the present study are generally similar to those found in an extensive survey of Sable Island groundfish during 1986–89 (McClelland et al. 1990). Longhorn sculpin and sea raven were again among the most heavily infected host species. The absence of sealworm from capelin and northern sand lance is not surprising, as these species feed pelagically, while sealworm infections seemed to be confined to benthic consumers and demersal piscivores. Moreover, with the exception of sealworm larvae found in freshly ingested northern sand lance from stomachs of grey seals from inshore Nova Scotia (McClelland et al. 1990), there are no records of *P. decipiens* in either capelin or northern sand lance. The absence of sealworm from winter flounder examined herein concurs with McClelland et al.'s (1990) report of extremely low levels of infection in winter flounder (single nematode infections in 2 of 174) from Sable Island Bank.

Abundance of *P. decipiens* increased with length of longhorn sculpin, American plaice, sea raven, and yellowtail flounder hosts. This trend was not apparent in our Atlantic cod samples but has frequently been evident in other surveys (Templeman et al. 1957; McClelland et al. 1983a, 1983b, 1990). This discrepancy can probably be attributed to the narrow size range of Atlantic cod examined herein; almost 90% were ⩽30 cm and none exceeded 40 cm in length. Increases in the level of sealworm infection in Atlantic cod seem to be associated with a change in diet from invertebrates to fish, as the parasites are far more numerous in the larger piscivorous fish (McClelland et al. 1990). Serial transmission of sealworm from fish to fish has been demonstrated in Atlantic cod (Scott 1954) and brook trout (*Salvelinus fontinalis*) (Burt et al. 1990). The fact that levels of *C. wegeneri* infection increase with host length in yellowtail flounder, winter flounder, longhorn sculpin, and sea raven suggests that the acanthocephalan, like *P. decipiens*, is long-lived in the fish host and is transferred from fish to fish in a manner similar to sealworm. *Corynosoma wegeneri* may therefore increase through cumulative reinfection, with larger fish consuming greater quantities of cystacanths by preying on larger, more heavily infected fish.

The invertebrate intermediate hosts of *C. wegeneri* are not known, but probably include amphipods (Petrochenko 1956). *Pseudoterranova decipiens* has been found in amphipods (Val'ter 1978, 1987; McClelland 1990), isopods (Bjorge 1979), shrimp (Uspenskaja 1960), mysids (Scott and Black 1960), and polychaetes (Val'ter and Popova 1974). There are no records of sealworm from invertebrates on Sable Island Bank, although we are presently examining invertebrates from that vicinity. Preliminary results have shown mysids (*Neomysis americana*) from Sable Island ponds to be infected with *P. decipiens* (Marcogliese 1992).

McClelland et al. (1990) noted that, among flatfishes, the species with the largest gapes also have the heaviest sealworm infections. Gape size may also be important in determining the relative abundances of *C. wegeneri* in yellowtail and winter flounder. Yellowtail flounder have the larger gape and were

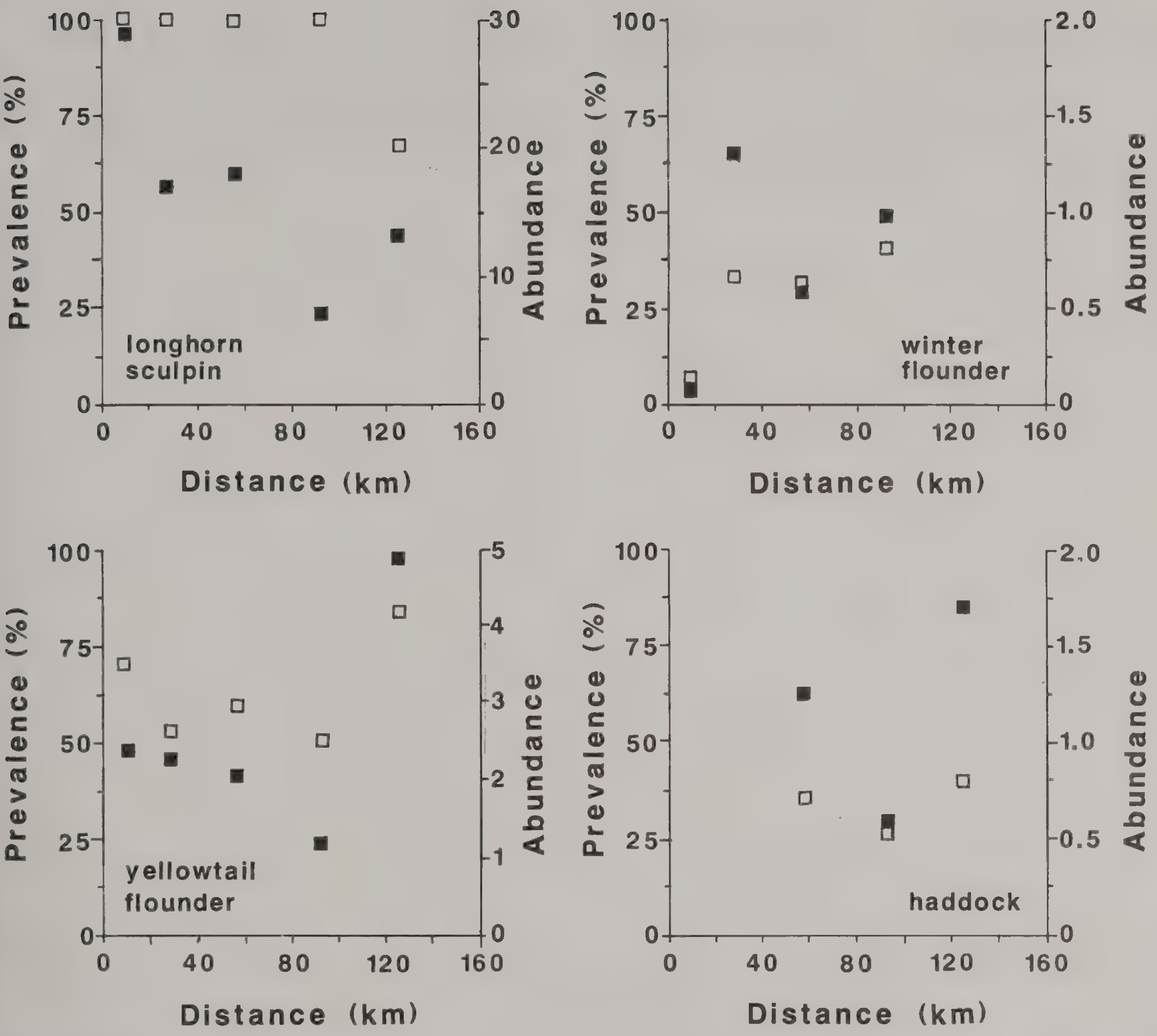

FIG. 3. Prevalence (open squares) and abundance (closed squares) of *C. wegeneri* in longhorn sculpin, yellowtail flounder, winter flounder, and haddock caught at five stations along a transect on Western and Sable Island banks in May 1990. Horizontal axis indicates distance from Sable Island.

more heavily parasitized than winter flounder in all length strata (Fig. 2). Winter flounder ≤20 cm in length which were uninfected were perhaps incapable of ingesting the invertebrate intermediate host of *C. wegeneri*.

Sable Island is the site of the largest concentration of grey seals in eastern Canada, and the population has increased exponentially between 1962 and 1988 (Zwanenburg and Bowen 1990). Coincidently, abundance of sealworm has also increased in groundfish populations on the Scotian Shelf (McClelland et al. 1983b, 1987, 1990). This study demonstrates that sealworm infection levels in small fishes collected close to Sable Island exceed those previously reported (McClelland et al. 1983b, 1985, 1990) in fish of the same species and size from Sable Island Bank and are greater than levels found in fish collected further from the island. The differences probably reflect the resident nature of small fish, which may remain close to Sable Island and acquire much higher infections than those found more distant from the island. Negative correlations between distance from Sable Island and sealworm abundances in longhorn sculpin and yellowtail flounder were statistically significant. The increasing levels of *P. decipiens* infection in groundfish with proximity to Sable Island are clearly attributable to the resident colony of grey seals, which are important definitive hosts of the parasite.

Similarly, in one host species, longhorn sculpin, there was a significant negative correlation between abundance of cystacanths of the grey seal parasite *C. wegeneri* and distance from Sable Island. In addition, the growing prevalence and abundance of *C. wegeneri* in Scotian Shelf groundfish, evident in comparisons of data from present and earlier studies, further

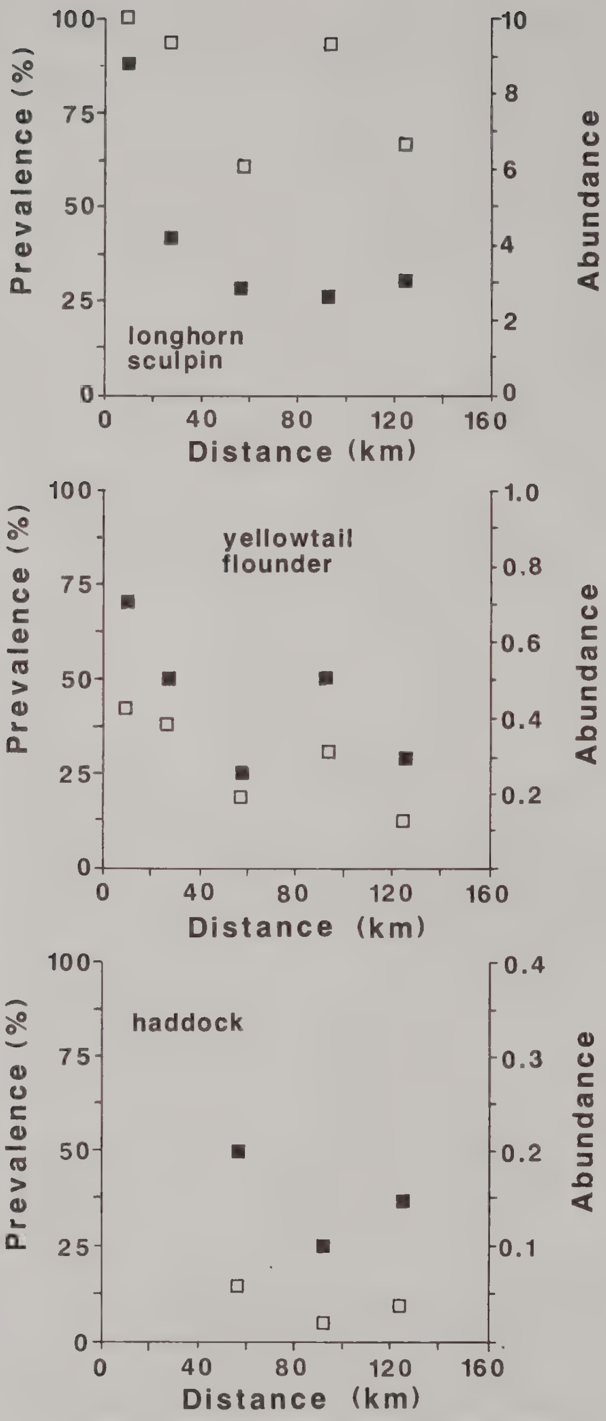

FIG. 4. Prevalence (open squares) and abundance (closed squares) of *P. decipiens* in longhorn sculpin, yellowtail flounder, and haddock caught at five stations along a transect on Western and Sable Island banks in May 1990. Horizontal axis indicates distance from Sable Island.

support our contention that the increasing population of grey seals on Sable Island has an impact on abundance of larval seal parasites in groundfish.

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Chronic Toxicity and Metabolism of Cd and Zn in Juvenile Minnows (*Phoxinus phoxinus*) Exposed to a Cd and Zn Mixture

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Wicklund Glynn, A., C. Haux, and C. Hogstrand. 1992. Chronic toxicity and metabolism of Cd and Zn in juvenile minnows (*Phoxinus phoxinus*) exposed to a Cd and Zn mixture. Can. J. Fish. Aquat. Sci. 49: 2070–2079.

Minnows (*Phoxinus phoxinus*) were exposed in the laboratory to 3 nM Cd (Cd group), 2000 nM Zn (Zn group), or to both metals (CdZn group) in soft water for 142 d. A fourth group was kept with no metals added to the water (Low group). After 80 d, the Cd and Zn groups were statically exposed to ^{109}Cd and ^{65}Zn, respectively, for 24 h. The CdZn group was exposed to both tracers. Fish were sampled for 61 d after the tracer exposure. At the end of the experiment, an increased metallothionein level was detected in the kidney of fish exposed to the metal mixture (Low group: 0.14 nmol/g fish; CdZn group: 0.54 nmol/g fish). However, the fish did not acquire tolerance to the metals because mortality continued at a constant rate during the whole experiment. Metabolism of Cd and Zn was altered in fish exposed to the metal mixture compared with fish exposed to Cd or Zn alone. The main effect was a Zn-induced increase in Cd turnover rate in the fish. Nevertheless, the toxic action of metals was additive, since mortality at the end of the experiment was 24, 32, and 54% in the Zn, Cd, and CdZn groups, respectively.

En laboratoire, des ménés (*Phoxinus phoxinus*) ont été exposés à 3 nM Cd (Cd), à 2000 nM Zn (Zn) ou aux deux métaux (CdZn) dans l'eau douce pendant 142 jours. Un quatrième groupe a été laissé dans de l'eau dans laquelle des métaux n'avaient pas été ajoutés (groupe à faible concentration). Au bout de 80 jours, les groupes exposés au Cd et au Zn ont été exposés de manière statique à du ^{109}Cd et du ^{65}Zn, respectivement, pendant 24 h. Le groupe exposé au CdZn a été exposé aux deux traceurs à la fois. Les groupes de poissons ont été soumis à des échantillonnages pendant 61 jours après l'exposition aux traceurs. À la fin de l'expérience, on avait détecté une augmentation de la concentration rénale de métallothionéine chez les poissons exposés aux deux métaux (groupe à faible concentration : 0,14 nmol/g poisson; groupe CdZn : 0,54 nmol/g poisson). Toutefois, le poisson n'a pas acquis de tolérance aux métaux, puisque la mortalité continuait d'être observée à un taux constant durant toute la durée de l'expérience. À comparer aux sujets exposés au Cd ou au Zn uniquement, le métabolisme du Cd et du Zn chez les sujets exposés aux deux métaux à la fois a été modifié. L'accélération du taux de renouvellement du Cd, attribuable au Zn, a été le principal effet observé. Néanmoins, l'action toxique des métaux était additive puisque la mortalité à la fin de l'expérience était de 24, 32, et 54 % chez les groupes exposés au Zn, au Cd et au CdZn, respectivement.

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In the natural environment, metals are often present as mixtures. Studies on toxicity of metal mixtures to fish indicate that mixtures might have additive or antagonistic effects (Eaton 1973; Finlayson and Verrue 1982; Roch and McCarter 1984), probably depending on fish species and life stage, water quality, and metal concentrations. Antagonistic effects of metal mixtures may be due to a changed metabolism of the metals caused by metal–metal interactions. Possible interactive effects on metal metabolism are alterations of (1) uptake, (2) organ distribution, (3) intracellular distribution, and (4) elimination. Metal–metal interactions and the possibility of fish acquiring tolerance towards metal mixtures should be taken into account when biological effects of metals are studied.

Preexposure of fish to sublethal levels of heavy metals may cause an increased level of metallothionein (MT) or MT-like proteins in the fish and a subsequent higher tolerance to acute levels of heavy metals (Benson and Birge 1984; Klaverkamp et al. 1984; Kito et al. 1986). However, results also indicate that preexposure may decrease the heavy metal uptake and accumulation in fish (Bradley et al. 1985; Wicklund Glynn and Olsson 1991). In many of the metal tolerance studies, high metal concentrations have been used during short-term toxicity testing (Klaverkamp et al. 1984). Moreover, the fish have often been preexposed to a single metal before the toxicity test (Duncan and Klaverkamp 1983; Kito et al. 1986; Hobson and Birge 1989). These are often not the conditions that fish encounter in nature.

In Sweden, the background levels of Cd and Zn are low (0.08–0.4 and 60–400 nM, respectively) (Borg 1983). However, some freshwater systems are heavily polluted because of mining activity. At the mouth of the river Dalälven, the Cd and Zn concentrations are ≃0.25 and 460 nM, respectively. Extremely high Cd and Zn levels have been registered further

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TABLE 1. Cd and Zn concentrations (mean ± SD (*N*)) in the water during the experiment.

Group	Cd (nmol/L)	Zn (nmol/L)
Low	<0.3	400 ± 200 (5)
Cd	2.7 ± 0.4 (9)	600 ± 100 (6)
Zn	<0.3	2100 ± 400 (9)
CdZn	2.8 ± 0.3 (9)	2300 ± 300 (9)

up in the drainage basin (2–37 and 300–40000 nM, respectively) (Lindeström 1991). Fish still exist in these waters, although the species composition is abnormal in some instances. This indicates that fish have acquired tolerance to the metals.

The aim of this study was to investigate the effects of a Cd and Zn mixture on the metabolism and chronic toxicity of the metals in juvenile minnows (*Phoxinus phoxinus*). The study also addressed the possibility of fish acquiring tolerance to the metals and the involvement of MT in the modulation of metal toxicity to fish.

Materials and Methods

Holding Conditions during the Experiment

Juvenile minnows were caught in the wild and held for 6 mo before the experiment begun, as described by Wicklund Glynn and Olsson (1991). Fish were held in soft water (unchlorinated tap water/deionized water, 1/10, conductivity ∓ 50 µS, Ca = 0.2 mM, Na = 0.07 mM) both during holding and the experiment. Fish (0.2–0.6 g body weight) were transferred to the laboratory and the experimental groups (≈250 fish/group) were held separately, each in a 10-L plastic aquarium with a water flow of 30 L/24 h for 1 wk before the experiment begun. A net basket in each aquarium was used to avoid contact between fish and debris on the bottom, and the water was continuously aerated inside the basket.

The experimental period of 142 d consisted of three parts: a preexposure period (80 d), a tracer exposure period (24 h), and a posttracer exposure period (61 d). During the preexposure and posttracer exposure periods, each group was held separately in 10-L aquaria, and during the tracer exposure period the groups were separately exposed to ^{109}Cd and/or ^{65}Zn, each in a 4-L aquarium with a net basket.

The metals were added from stock solutions ($CdNO_3$ and $ZnSO_4$, analytical grade, Merck, Germany) as described by Wicklund Glynn (1991). The fish were fed commercial fish food twice a day (Tetraanimin, Tetrawerk, Germany) and were transferred to clean aquaria once a fortnight. The water temperature was 14 ± 1°C and the photoperiod was that natural to latitude 60° (≈15–20 h light/4–9 h dark).

Water samples (200 mL) were taken from each aquarium for metal analysis once a fortnight, preserved by addition of 2 mL of 4 mM H_2SO_4 (suprapur, Merck, Germany), and stored at 4°C. The measured values of Cd and Zn were 90–93 and 105–115% of the nominal concentrations, respectively (Table 1). The Cd concentration in the water of the Low group was below the detection limit (<0.3 nM), and the mean Zn concentration was 400 nM (Table 1). The relatively high Zn concentration in the experimental water was unexpected and not intended. However, it was five times lower than the concentration that the Zn and CdZn groups were exposed to and within the upper range of background levels in unpolluted Swedish freshwaters.

Metal and Tracer Exposures

Preexposure (80 d)

The Cd group was preexposed to 3 nM Cd, the Zn group to 2000 nM Zn, and the CdZn group to a mixture of Cd and Zn. The Low group was exposed to ≈400 nM Zn and <0.3 nM Cd. Groups (≈250 fish/group) were held separately in 10-L aquaria.

Tracer exposure (24 h)

Groups were exposed to the tracers separately in 4-L aquaria. The metal concentrations in the water were the same as during preexposure. The Cd group was statically exposed to ^{109}Cd, the Zn group to ^{65}Zn, and the CdZn group to both tracers ($^{109}CdCl_2$, 14 000 cpm/mL, 3 nM Cd; $^{65}ZnCl_2$, 1800 cpm/mL, 2000 nM Zn; carrier free, NEN Products, USA). The Low group was not exposed to the tracers.

Posttracer exposure (61 d)

The fish were rinsed in tracer-free water for 1 h and transferred back to the 10-L aquaria. Concentrations of Cd and Zn in the water were the same as during the preexposure and tracer exposure periods.

Tissue Sampling and Analysis

The entire gill basket, liver, kidney, and rest of the body were sampled from 5–10 fish in the Cd, Zn, and CdZn groups 1 h and 1, 2, 4, 6, 9, 15, 20, 27, and 34 d after the tracer exposure. Thereafter, the Cd and Zn groups were sampled 48 and 61 d after the tracer exposure whereas the CdZn group was sampled 54 and 61 d after the tracer exposure. The sampling was ended on day 61 because no fish were left in the CdZn group (after 142 d of metal exposure). Each organ was placed in a plastic capsule and analysed for radioactivity in a Searle gamma-counter (model 1185). The results were corrected for radioactive decay and expressed as picomoles or nanomoles per gram of whole fish weight because of difficulties in wet weight determination of the tissues (uncertain because of low weights, 0.5–20 mg).

Intracellular Tracer Distribution

The entire gill basket was removed from five fish in the Cd, Zn, and CdZn groups 1 h and 15 and 16 d after the tracer exposure. The entire liver and kidney were removed after 15 and 61 d. The tissue preparation and gel chromatography (Sephadex G-75, Pharmacia/LKB, Sweden) were performed as described by Wicklund Glynn and Olsson (1991). The ^{109}Cd content in the gills, liver, and kidney was determined in the two pellets obtained after centrifugation at 12 000 × *g* (pellet 1, nuclear/mitochondrial fraction) and 100 000 × *g* (pellet 2, microsomal fraction), in the ultrasupernatant obtained after the last centrifugation (cytosolic fraction), and in the fractions obtained after chromatography of the ultrasupernatant. The recovery after preparation of the tissues did not differ among the Cd, Zn, and CdZn groups, and 98 ± 8% (*N* = 12), 90 ± 8% (*N* = 12), and 89 ± 11% (*N* = 12) of the ^{109}Cd was recovered in the gills, liver, and kidney, respectively.

The ^{109}Cd eluted from the Sephadex G-75 column was mainly detected in two peaks. One peak, called high molecular weight (HMW) fraction, eluted between the void volume, and the second peak (Cd-BP) eluted concomitant with rabbit MT. A small part of the tracer that eluted after the second peak was called the low molecular weight (LMW) fraction. The recovery of ^{109}Cd after gel chromatography was not significantly different between the Cd and CdZn groups (gills: 43 ± 7% ($N = 11$); liver: 85 ± 20% ($N = 12$); kidney: 77 ± 9% ($N = 11$).

The distribution of ^{65}Zn in the gills was calculated from the total ^{65}Zn content in the organ before homogenization and from the ^{65}Zn content in pellets 1 and 2 after centrifugation.

MT and Metal Determinations

The entire gill basket, liver, and kidney from five fish per group were sampled from the Low, Cd, Zn, and CdZn groups for MT analysis at the end of the tracer exposure (81 d) and on day 61 posttracer exposure (142 d). The organs were sampled and prepared as described by Wicklund Glynn and Olsson (1991). In short, tissue homogenates were centrifuged at 12 000 × g for 5 min (4°C) and the supernatant was heat denatured at 95°C for 5 min. Denatured samples were centrifuged at 12 000 × g for 5 min. MT in the supernatant was determined by differential pulse polarography (DPP) at 20°C (PARC model 174 analyzer, PARC/EG & G model 303 SMDE) as described by Olsson and Haux (1986). Whole organs were sampled and analysed, but the precision of the weight determination was uncertain because of low weights (0.5–20 mg). Tissue levels of MT were therefore expressed as nanomoles of MT per gram of whole body weight. All samples were analysed on the same occasion to avoid analytical differences.

The gill basket, liver, and kidney from six fish per group were sampled from the Low, Cd, Zn, and CdZn groups at the end of the tracer exposure (81 d) and at day 61 posttracer exposure (142 d) for metal analysis. Organs of each type from each group of fish were pooled in preweighed, acid-washed borosilicate glass tubes and weighed before storage at −20°C. The tissue preparation and Cd analysis were performed as described by Wicklund Glynn (1991). Zn was analysed in a plasma emission spectrometer (Thermo Jarrell, ASH/ICAP 61) and Cd was analysed in an atomic absorption spectrophotometer (Perkin Elmer 5000) with a graphite furnace (MGA-400) at the Swedish Agricultural Chemical Laboratory, Uppsala, Sweden. All samples were analysed on the same occasion to avoid analytical differences.

Calculations and Statistical Analysis of the Results

Total tracer content in tissues and the specific activity of the tracers in the water were used to calculate the amount Cd and Zn retained in the fish during the tracer exposure. The constants obtained from the nonlinear regression analysis (Procedure NLIN, SAS Inc., Cary, NC) of the tracer accumulation and elimination were used for statistical evaluation of the results (Wicklund Glynn and Olsson 1991).

A biexponential elimination equation showed a better fit than a monoexponential equation to the ^{109}Cd elimination from the whole body, gills, and rest of the body and the ^{65}Zn elimination from the gills, liver, and kidney. The biexponential elimination curve is a summation of two monoexponential elimination curves, one with a rapid elimination half-time and one with a slow elimination half-time:

$$(1) \quad C = C_0 \cdot (f \cdot e^{\ln 2/t_1 \cdot t} + (1-f) \cdot e^{-\ln 2/t_2 \cdot t})$$

where C = the amount of tracer in the tissue at $t = x$ d, C_0 = the amount of tracer in the tissue at $t = 0$ d, f = the relative amount of rapidly eliminated tracer, t_1 = the rapid elimination half-time, $(1-f)$ = the relative amount of slowly eliminated tracer, t_2 = the slow elimination half-time.

The goodness-of-fit of the biexponential equation to the elimination results was checked against the goodness-of-fit of a monoexponential equation (represented by fraction f in eq. 1). The residuals obtained after each regression analysis were plotted with the fitted curve as a reference 0-line. The residuals of the monoexponential fit showed a U-shaped distribution pattern around the reference line, and this trend was removed by fitting the biexponential equation to the results for which the residuals were not patterned.

The ^{109}Cd accumulation in the liver and kidney was described by an exponential accumulation equation:

$$(2) \quad C = C_a \cdot (1 - e^{-\ln 2/t_a \cdot t})$$

where C_a = the asymptote of the accumulation curve and t_a = the accumulation half-time.

A two-tailed t-test for samples exhibiting heterogeneity of variance (Wynne 1982) was used to compare elimination and accumulation half-times obtained by regression analysis. Nonparametric tests were used to compare results from single sampling occasions because of the low number of observations. The Kruskal–Wallis test was used to compare results when more than two groups were tested. The Mann–Whitney U-test was used when two groups were tested. The level of significance was $p < 0.05$ in all tests.

Results

There was no significant difference in body weight among the Low, Cd, Zn, and CdZn groups at any of the sampling occasions, and fish showed little growth (Kruskal–Wallis test). The median weight at the first sampling ranged between 189 and 245 mg and at the last sampling between 210 and 286 mg (Table 2). There were no significant differences in the organosomatic indices between the groups (Table 2) (Kruskal–Wallis test).

Mortality

After 142 d in the laboratory, only 10% of the fish in the Low group had died (Fig. 1). Mortality of the Cd- and Zn-exposed fish occurred at a nearly constant rate during the experiment. The mortality of fish exposed to the metal mixture varied between more than additive and less than additive in relation to the mortality of fish exposed to the single metals. Variation was not large, and overall the toxicity of the metal mixture appeared to be additive. After 142 d, 54% of the fish in the CdZn group had died whereas 32% in the Cd group and 24% in the Zn group had died (Fig. 1).

Metals and MT in the Fish

Since the Cd and Zn concentrations were determined in one pooled sample of each tissue, no statistical analysis of the results could be done. However, the results give an indication of the body burden of the metals.

Cd

After 80 d of metal exposure, the Cd levels in the pooled gill samples were 19–33 times higher in the Cd and CdZn groups than in the Low and Zn groups (Table 3). The concentrations were 8.6–22 and 3.4–6.2 times higher in the liver and kidney samples, respectively, in the Cd and CdZn groups than in the Low and Zn groups. After 142 d, the Cd levels had decreased in the Low and Zn groups and also in gills of the CdZn group (Table 3). Cd levels remained consistently higher in the Cd and CdZn groups than in the Low and Zn groups.

TABLE 2. Body weight and organosomatic index (median (min–max)). A Kruskal–Wallis test showed that there were no significant differences between the groups on each sampling occasion ($p < 0.05$).

Group	Body weight[a] (mg)	Organosomatic index[b] Gills (%)	Liver (%)	Kidney (%)
Day 80				
Low	189 (161–344)	2.5 (2.1–3.1)	3.1 (1.9–3.9)	0.9 (0.5–1.2)
Cd	245 (188–330)	2.5 (2.1–3.0)	2.8 (2.7–4.1)	0.8 (0.7–1.2)
Zn	243 (118–389)	2.2 (2.0–3.2)	3.8 (1.9–5.8)	0.9 (0.6–1.5)
CdZn	244 (155–365)	2.1 (1.7–2.5)	2.0 (1.9–4.1)	0.9 (0.8–1.1)
Day 142				
Low	286 (224–725)	2.2 (1.5–2.5)	1.8 (0.7–3.4)	0.8 (0.8–1.0)
Cd	255 (171–378)	2.2 (1.6–2.5)	2.7 (2.3–4.0)	0.9 (0.6–1.2)
Zn	265 (166–310)	2.1 (1.6–2.3)	2.1 (1.8–2.9)	0.8 (0.6–1.2)
CdZn	210 (106–319)	2.0 (1.9–2.9)	2.8 (1.4–2.6)	1.0 (0.9–1.1)

[a] $N = 5$ for the Low group; $N = 10$ for the Cd, Zn, and CdZn groups.

[b] $N = 5$ for all groups.

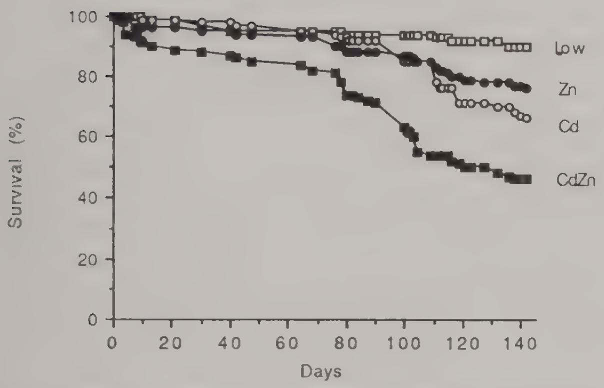

FIG. 1. Survival among juvenile minnows exposed to Cd (3 nM) or Zn (2000 nM) alone or as a mixture.

Zn

After 80 d of exposure, the Zn levels in the gills and kidney of the Zn and CdZn groups were 1.4–1.8 times higher than in the Low and Cd groups, and after 142 d, they were 2.0–3.1 times higher (Table 3). The levels in the liver were not markedly different among the groups. Between 80 and 142 d, Zn levels dropped in the gills and kidney of the Low, Cd, and Zn groups but increased in the CdZn group. The concentrations in the liver increased in the Cd and CdZn groups and decreased in the Low and Zn groups (Table 3).

MT

In this case, single organs were analysed, which made statistical analysis possible. After 80 d, the MT levels did not significantly differ between the Low group and the metal-exposed groups (Table 2) (Kruskal–Wallis test). After 142 d, the kidney of the CdZn group showed a significantly higher MT level than that of the Low group (Mann–Whitney *U*-test). MT levels significantly decreased between 80 and 142 d in all tissues of the Low group, in the gills of the Cd group, and in the kidney of the Zn group (Mann–Whitney *U*-test).

Tracer Retention, Redistribution, and Elimination

^{109}Cd retention

After 24 h of tracer exposure, the CdZn group had a significantly higher ^{109}Cd retention in the whole body, rest of the body (mainly muscle, bone, head, skin, and gastrointestinal tract), liver, and kidney than the Cd group (Table 4) (Mann–Whitney *U*-test).

^{109}Cd redistribution

After the tracer exposure, the content of ^{109}Cd in the liver and kidney increased 14–25 times, but the asymptote of the accumulation curve was not significantly different between the Cd and CdZn groups (Fig. 2) (*t*-test). The half-time of the ^{109}Cd accumulation in the kidney was significantly shorter for the CdZn group than for the Cd group (Table 5) (*t*-test).

^{109}Cd elimination

The whole body, gills, and rest of the body (mainly muscle, bone, head, skin, and gastrointestinal tract) eliminated ^{109}Cd at two different rates (see Materials and Methods: Calculations and Statistical Analysis of the Results). One ^{109}Cd elimination half-time was rapid, while the other was so slow that it was not possible to estimate from the results obtained during 61 d of elimination (Fig. 2). The CdZn group had a shorter rapid elimination half-time than the Cd group in the parts of the body studied (Table 5) (*t*-test). The rapid half-time ranged from 2.1 to 11.4 d, and 70–97% of the ^{109}Cd was eliminated from this pool (Table 5).

^{65}Zn retention

After 24 h of tracer exposure, the retention of ^{65}Zn did not vary between the Zn and CdZn groups, except that the gills of the CdZn group retained significantly less ^{65}Zn than those of the Zn group (Table 4) (Mann–Whitney *U*-test).

^{65}Zn elimination

The gills, liver, and kidney eliminated ^{65}Zn, but the ^{65}Zn content was so low in these organs that no marked whole-body ^{65}Zn elimination was evident (Fig. 3). Similarly, no elimination could be detected in the rest of the body. The elimination in gills, liver, and kidney was biphasic and the rapid half-time did not differ between the Zn and CdZn groups (Table 5) (*t*-test). Between 24 and 76% of the ^{65}Zn was lost with a rapid elimination half-time of 1.7–7.8 days. In the gills and liver, the percentage of rapidly eliminated ^{65}Zn was significantly lower in the CdZn group than in the Zn group (Table 5) (*t*-test).

Intracellular Tracer Distribution

^{109}Cd in the gills

Eighty to 85% of the branchial ^{109}Cd was detected in the cytosol at the end of the tracer exposure (Fig. 4A). The per-

TABLE 3. Cd, Zn, and MT levels in juvenile minnows exposed to Cd or Zn alone or to a mixture of the metals. Each Cd and Zn value represents a sample of six pooled tissues. MT analysis was done on single tissues and is presented as median (min–max) ($N = 4–5$). Low group: [Cd] < 0.03 nM, [Zn] = 500 nM; otherwise when Cd and/or Zn was added to the water, [Cd] = 3 nM and [Zn] = 2000 nM. bw = body weight.

	80 d			142 d		
Group	Cd (μg/g)	Zn (μg/g)	MT (nmol/g bw)	Cd (μg/g)	Zn (μg/g)	MT (nmol/g bw)
Gills						
Low	0.024	78	0.35 (0.33–0.66)	0.008	48	0.15 (0.12–0.22)[a]
Cd	0.78	76	0.47 (0.27–0.50)	0.33	54	0.12 (0.09–0.20)[a]
Zn	0.027	134	0.37 (0.28–0.49)	0.010	126	0.19 (0.13–0.33)
CdZn	0.51	116	0.28 (0.15–0.49)	0.065	150	0.62 (0.07–1.0)
Liver						
Low	0.035	23	0.88 (0.61–1.6)	0.022	18	0.57 (0.20–0.66)[a]
Cd	0.78	18	0.80 (0.43–1.3)	0.86	25	0.48 (0.27–1.1)
Zn	0.037	29	0.77 (0.48–1.6)	0.031	23	0.66 (0.34–0.85)
CdZn	0.32	21	0.61 (0.21–1.1)	0.86	45	0.94 (0.33–1.7)
Kidney						
Low	0.31	202	0.28 (0.20–0.51)	0.23	113	0.14 (0.09–0.22)[a]
Cd	1.93	198	0.29 (0.19–0.37)	1.94	143	0.26 (0.04–0.32)
Zn	0.48	322	0.42 (0.18–0.73)	0.23	282	0.14 (0.08–0.67)[a]
CdZn	1.64	289	0.43 (0.33–0.51)	1.44	316	0.54 (0.30–1.4)[ab]

[a] Significantly different from the day 80 level (Mann–Whitney *U*-test, $p < 0.05$).

[b] Significantly different from the Low group level (Mann–Whitney *U*-test, $p < 0.05$).

TABLE 4. ^{109}Cd and ^{65}Zn levels in minnows after a 24-h exposure in the water (median (min–max)). Cd group: [Cd] = 3 nM, [Zn] = 500 nM; Zn group: [Cd] < 0.03 nM, [Zn] = 2000 nM; CdZn group: [Cd] = 3 nM, [Zn] = 2000 nM.

Group	Whole Body	Gills	Liver	Kidney	Rest of body
			^{109}*Cd (pmol/g body weight)*		
Cd	14.5	4.3	0.032	0.033	8.3
	(6.1–19.9)	(1.3–11.7)	(0.025–0.044)	(0.027–0.085)	(4.6–13.8)
CdZn	22.0[a]	3.0	0.072[a]	0.081[a]	15.7[a]
	(9.9–27.0)	(1.3–10.8)	(0.032–0.14)	(0.038–0.16)	(4.7–24.9)
			^{65}*Zn (nmol/g body weight)*		
Zn	7.1	0.68	0.20	0.27	5.1
	(3.7–10.6)	(0.31–0.92)	(0.12–0.31)	(0.048–0.40)	(2.8–6.9)
CdZn	6.9	0.36[a]	0.18	0.18	5.5
	(3.5–8.3)	(0.21–0.48)	(0.092–0.23)	(0.13–0.28)	(2.8–7.0)

[a] Significantly different from the Cd or Zn group (Mann–Whitney *U*-test, $p < 0.05$, $N = 10$).

centage of ^{109}Cd in the cytosolic fraction significantly decreased during the period of tracer elimination whereas the percentage in the nuclear/mitochondrial fraction significantly increased (Kruskal–Wallis test). However, the particulate/cytosolic ^{109}Cd distribution was not significantly different between the Cd and CdZn groups (Mann–Whitney *U*-test).

At the end of the tracer exposure, the ^{109}Cd distribution in the cytosol of the gills was significantly different between the Cd and CdZn groups (Mann–Whitney *U*-test) (Fig. 4B). In the Cd group, 66% of the ^{109}Cd was present in the Cd-BP fraction and 30% in the HMW fraction. The ^{109}Cd binding pattern was reversed in the CdZn group, i.e. 34% was present in the Cd-BP fraction and 60% of the HMW fraction (Fig. 4B). These differences were still evident after 15 d of tracer elimination.

^{109}*Cd in the liver and kidney*

The distribution of ^{109}Cd in the liver and kidney was not significantly different between the Cd and CdZn groups (Fig. 4A) (Mann–Whitney *U*-test). Most of the ^{109}Cd was detected in the cytosolic fraction after 15 d of tracer accumulation (liver: 65–75%; kidney: 90–91%) (Fig. 4A). After 61 d of ^{109}Cd accumulation, the ^{109}Cd binding pattern was the same in the kidney. In the liver the percentage of ^{109}Cd in the cytosol had significantly increased to 90% in both groups. The percentage in the P1 fraction decreased from 16 and 23% in the Cd and CdZn groups, respectively, to 8% in both groups whereas the percentage in the P2 fraction decreased from 6 and 10% in the Cd and CdZn groups, respectively, to 2% in both groups (Fig. 4A) (Mann–Whitney *U*-test).

The ^{109}Cd binding pattern in the liver and kidney cytosol was not significantly different between the Cd and CdZn groups, except for a significantly lower percentage of tracer in the P2 fraction of the CdZn group after 15 d of accumulation (Fig. 4B) (Mann–Whitney *U*-test). At day 15 the majority of the ^{109}Cd in the kidney cytosol was recovered in the Cd-BP fraction (90–

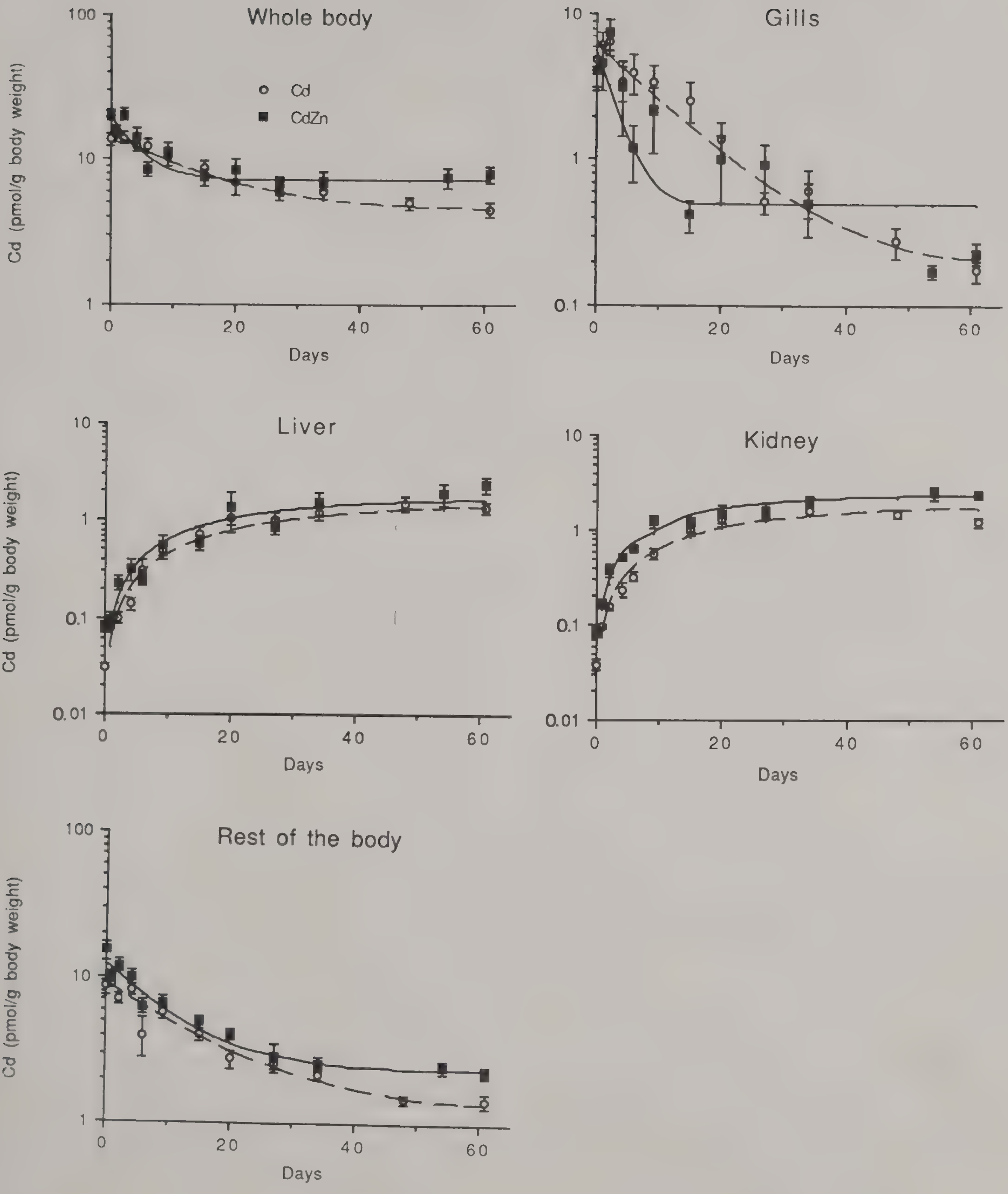

FIG. 2. ^{109}Cd elimination and redistribution in minnows during a 61-d posttracer exposure period in tracer-free water. A biexponential elimination equation and an exponential accumulation equation were fitted to the elimination and accumulation results, respectively, by the method of least squares (see Materials and Methods). The results are presented as mean ± SE. Vertical scales are logarithmic.

TABLE 5. Half-time (d) of rapidly eliminated (elim) ^{109}Cd (whole body, gills, and rest of the body) or ^{65}Zn (gills, liver, and kidney) and accumulation (acc) half-time (d) of ^{109}Cd (liver and kidney) after a 24-h exposure to ^{109}Cd and/or ^{65}Zn [Cd] = 3 nM, [Zn] = 2000 nM). Half-times were estimated from the regression analysis of tracer elimination and accumulation during a 61-d postexposure period in tracer-free water. Percentage rapidly eliminated tracer in parentheses. No elimination of ^{65}Zn could be detected in whole body and rest of the body. Values are mean ± SE; N = 120 (Cd), 130 (Zn), and 99 (CdZn). nd = not determined.

	^{109}Cd		^{65}Zn	
Organ	Cd	CdZn	Zn	CdZn
Whole body (elim)	9.7 ± 1.8 (70 ± 3%)	3.0 ± 0.9[a] (64 ± 4%)	nd	nd
Gills (elim)	7.7 ± 1.0 (97 ± 1%)	2.1 ± 0.6 (93 ± 2%)	2.1 ± 0.5 (66 ± 3%)	1.7 ± 0.9 (47 ± 7%)[a]
Liver				
acc	22.4 ± 4.4	16.3 ± 4.5		
elim			7.8 ± 1.3 (76 ± 2%)	4.8 ± 1.7 (62 ± 5%)[a]
Kidney				
acc	17.5 ± 2.2	11.5 ± 1.7[a]		
elim			3.5 ± 2.5 (29 ± 7%)	2.6 ± 2.4 (24 ± 8%)
Rest of body (elim)	11.4 ± 1.8 (88 ± 2%)	6.5 ± 1.1[a] (81 ± 2%)[a]	nd	nd

[a] t-test, $p < 0.05$.

96%). This pattern was not significantly changed after 61 d of accumulation. Contrary to that, between 15 and 61 d of accumulation the percentage in the HMW fraction of the liver significantly decreased from 58 and 73% to 8 and 6% in the Cd and CdZn groups, respectively (Mann–Whitney U-test). The percentage in the Cd-BP fraction significantly increased from 35 and 18% in the Cd and CdZn groups, respectively, to 90 and 92% (Fig. 4B) (Mann–Whitney U-test).

^{65}Zn in the gills

^{65}Zn distribution in the branchial ultrasupernatant and in the liver and kidney could not be studied because the count rates were too low. After the tracer exposure, most of the ^{65}Zn in the gills was detected in the nuclear/mitochondrial and cytosolic fractions (43–48%) in both the Zn and CdZn groups (Fig. 5). In both groups, the percentage in the nuclear/mitochondrial fraction significantly increased and the percentage in the cytosolic fraction decreased after 15 d of tracer elimination (Mann–Whitney U-test). However, the change was significantly greater in the Zn group than in the CdZn group (Mann–Whitney U-test). After 61 d of elimination, the ^{65}Zn binding pattern was the same as after 15 d (Fig. 5).

Discussion

Mortality and MT

The mortality in the Low group was 10% after 142 d. Considering that the fish were caught in the wild and held in the laboratory under high population density conditions, the mortality was not considered unduly high in the Low group.

Cd and Zn acted additively on the mortality of juvenile minnows. Antagonistic interactions between metals have been related to increased levels of cytosolic metal-binding proteins, such as MT (Bradley et al. 1985; Kito et al. 1986). MT is supposed to increase the metal tolerance of fish by binding and detoxifying deleterious metal ions. The increased MT content in the kidney of the minnows exposed to the metal mixture did not reduce mortality. However, the gill is a major target organ for Cd and Zn toxicity (Karlsson-Norrgren et al. 1985; Spry and Wood 1985), and induction of MT in the kidney would not protect the fish if the gill was the site for toxic action of the metals. In the minnows, Cd and Zn exposure did not cause a significantly increased MT level in the gills, although Cd levels were 19–33 times higher and Zn levels 2–3.1 times higher. It is possible that the increase in MT level in the kidney occurred too late for a protective effect to be detected during the experiment.

It is obvious, however, that Cd and Zn alone were toxic to the juvenile minnows at levels that did not cause an induction of MT. The basic experimental water had a Zn concentration of ≈400 nM, and it is possible that the Low group had already reached their maximum MT induction in the gills and liver. The fish in the Cd, Zn, and CdZn groups in that case would not be able to respond to the metal exposure with a further increase of the levels of MT in these organs. However, the level of Zn decreased in the gills of the Low group between 80 and 142 d, which indicates that the Zn load of the fish was not high enough to cause an accumulation of Zn in the organ. Moreover, the levels of Zn in the liver were stable during the experiment, and the levels of MT in gills and liver in the Low group decreased between 80 and 142 d. The increased level of MT in the kidney of the CdZn group also argues against the possibility of a maximum MT induction already reached by the Low group.

The inability of the fish to produce MT in response to metal exposure may partly explain why the minnow is sensitive to Cd and Zn (Bengtsson 1974). Juvenile fish are generally more susceptible to metals than adult fish (Mance 1987). In a previous study, adult minnows showed a lower mortality than juvenile fish when exposed to 3 nM Cd for 150 d (Wicklund Glynn and Olsson 1991). Also, the Cd-exposed adult minnows did not show an increased MT level in the gills, liver, and kidney. This suggests that the lower Cd sensitivity of the adult fish, compared with the juvenile fish, was not caused by differences in the ability to synthesize MT.

The decrease in metal and MT levels in some of the organs between 80 and 142 d is difficult to explain. All samples were randomly analysed at the same time, which means that analytical differences can be excluded. An effect of growth

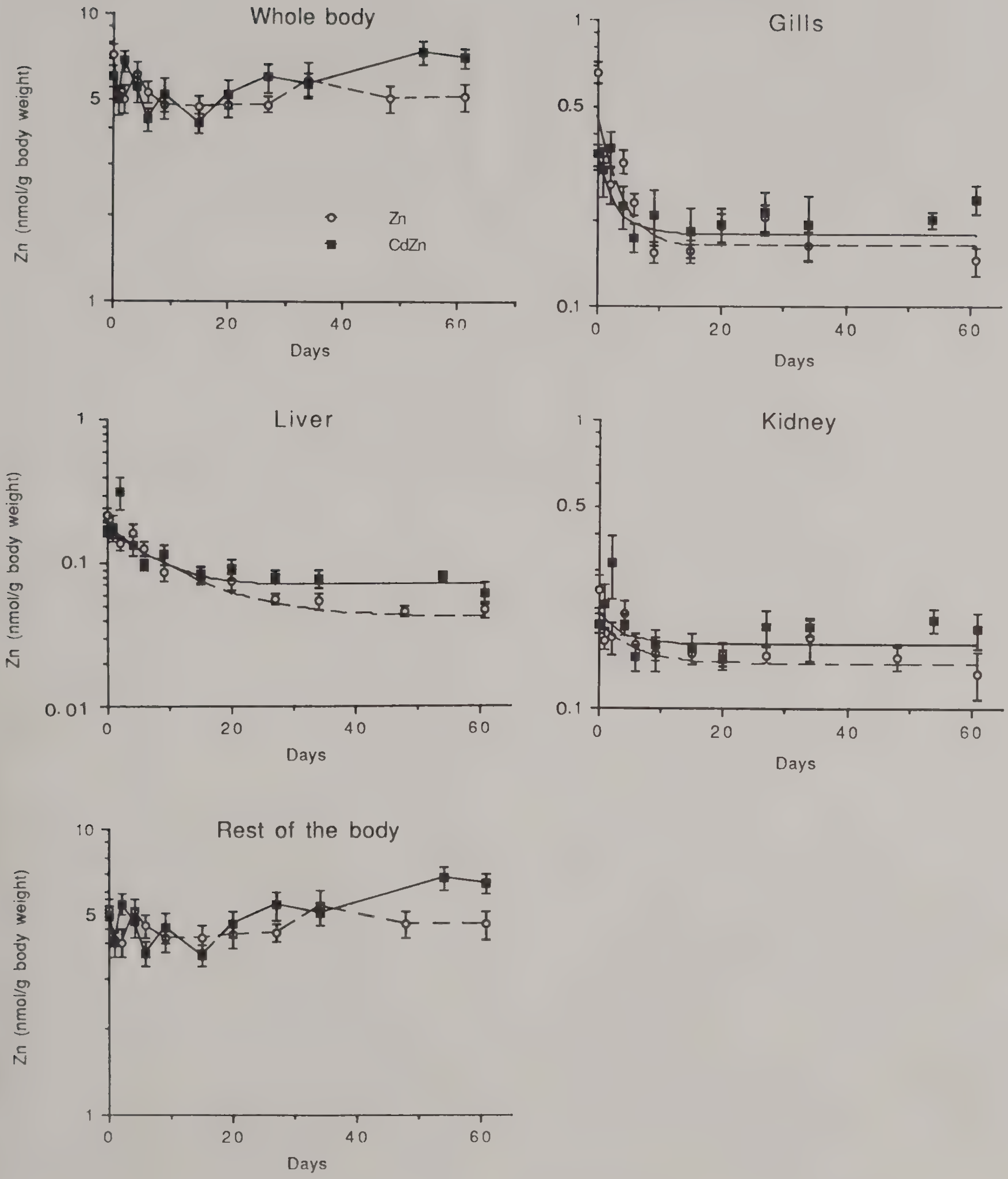

FIG. 3. ^{65}Zn elimination in minnows during a 61-d postexposure period in tracer-free water. A biexponential elimination equation was fitted to the gills, liver, and kidney ^{65}Zn results by the method of least squares (see Materials and Methods). The results are presented as mean ± SE. Vertical scales are logarithmic.

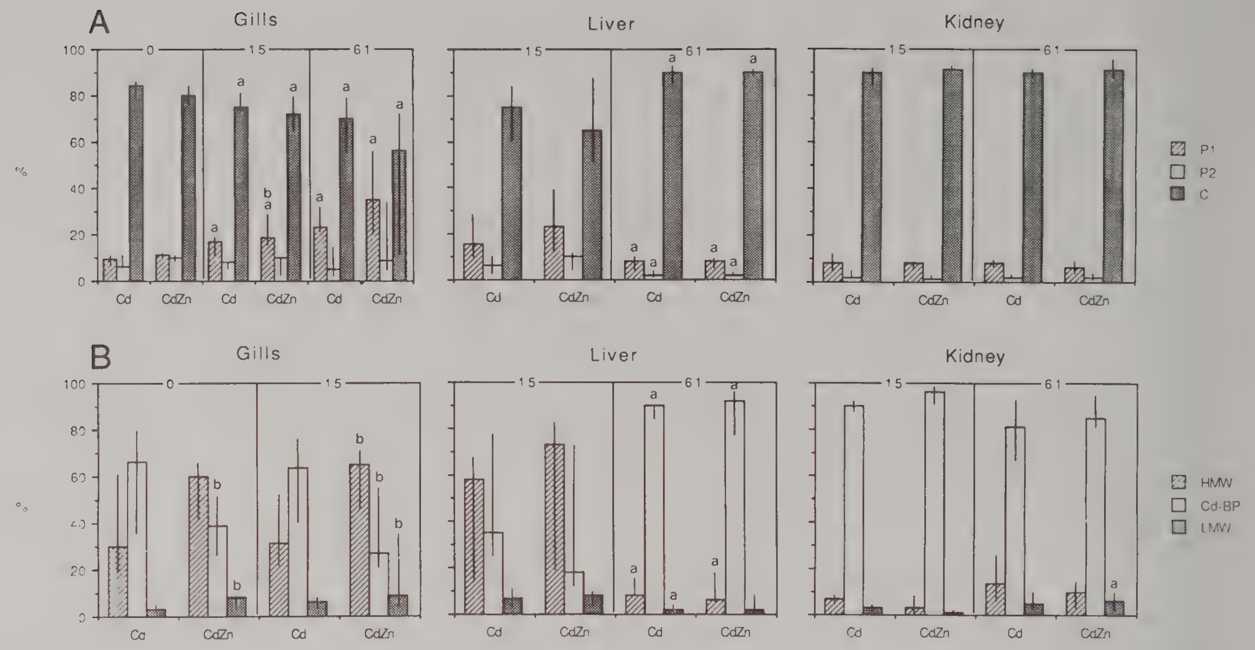

FIG. 4. Intracellular distribution of ^{109}Cd (median (min–max)) in gills (N = 4–5, liver (N = 3–5), and kidney (N = 4–5) of minnows at the end of a 24-h tracer exposure period and after 15 and 61 d in tracer-free water. (A) P1 = nuclear/mitochondrial fraction; P2 = microsomal fraction; C = cytosol; a = significantly different from the day 0 results (Kruskal–Wallis test, $p < 0.05$); b = significantly different from the Cd results (Mann–Whitney U-test, $p < 0.05$). (B) Cytosol, consisting of HMW, Cd-BP, and LMW fractions. a = significantly different from the day 0 results (Mann–Whitney U-test, $p < 0.05$); b = significantly different from the Cd results (Mann–Whitney U-test, $p < 0.05$).

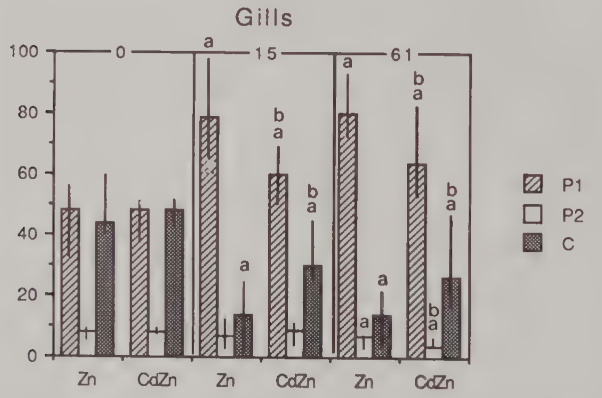

FIG. 5. Intracellular distribution of ^{65}Zn (median percent total; error bar = range) in gills (N = 4–5) of minnows at the end of a 24-h tracer exposure and after 15 and 61 d of tracer elimination. P1 = nuclear/mitochondrial fraction; P2 = microsomal fraction; C = cytosol; a = significantly different from the day 0 results (Kruskal–Wallis test, $p < 0.05$); b = significantly different from the Zn results (Mann–Whitney U-test, $p < 0.05$).

dilution is not probable because the fish did not grow significantly during the experiment. A possibility is that the fish had accumulated the metals before capture. Thus, the decrease could be due to a slow elimination of the metals from the organs. Another factor that should be considered is the presence of hormones such as corticosteroids, which affect the levels of MT and thus possibly also the levels of Cd and Zn (Hyllner et al. 1989).

Effects of Zn on ^{109}Cd Metabolism

The ^{109}Cd turnover in the minnows was the same as previously reported, with a relatively rapid turnover in the gills and a redistribution of tracer to the liver and kidney (Wicklund Glynn 1991; Wicklund Glynn and Olsson 1991). An increase in the external Zn concentration from ≈400 to 2000 nM did not reduce the ^{109}Cd retention in the gills after the 24-h tracer exposure. This suggests that the branchial uptake of Cd was not affected by Zn at this concentration. Also, Zn had no influence on the distribution of ^{109}Cd between the branchial cytosolic and particulate fractions. However, Zn seemed to have an ability to reduce the binding of ^{109}Cd to the Cd-BP fraction in the gills, presumably MT, thus causing an increased binding of ^{109}Cd to the HMW and LMW fractions. This effect of Zn is hard to explain, since Cd^{2+} has a higher affinity for MT than Zn^{2+} (Day et al. 1984; Waalkes et al. 1984). However, it may be possible that a high amount of intracellular Zn^{2+}, due to the Zn exposure, reduced the amount of Cd^{2+} bound to MT during the tracer exposure.

The turnover rate of Cd was increased by Zn as shown by the more rapid ^{109}Cd elimination by the gills and accumulation in the kidney. The higher percentage of branchial ^{109}Cd bound to the HMW and LMW fractions in the CdZn group than in the Cd group may have caused a higher availability of the tracer for transfer from the gills to the internal organs. However, a general mobilizing effect of Zn on intracellular Cd in the gills could also explain the higher ^{109}Cd turnover in the CdZn group. At the end of the experiment, the branchial Cd level was lower in the fish exposed to the Cd and Zn mixture than in the Cd-exposed fish. This could be a result of the Zn-induced increase in the Cd elimination rate in the gills. Similarly, Zn has been found to increase the branchial ^{109}Cd elimination rate in the zebrafish (*Brachydanis rerio*) (Wicklund et al. 1988).

In contrast with the gills, the intracellular distribution of ^{109}Cd in the liver and kidney was not altered by Zn. This suggests that there are differences in the intracellular metabolism of the metals between the gills and the liver and kidney.

Effects of Cd on ^{65}Zn Metabolism

The turnover of ^{65}Zn in the juvenile minnows was similar to that described for juvenile minnows in an earlier study, with a rapid turnover in the gills, liver, and kidney and a slow turnover in the whole body (Wicklund Glynn 1991). Exposure to Cd altered the ^{65}Zn metabolism in the gills and liver by decreasing the percentage of rapidly eliminated tracer. Moreover, in the gills, the CdZn group showed a more rapid decrease of ^{65}Zn in the cytosolic fraction than the Zn group, suggesting that Cd can alter Zn metabolism in the minnow.

Fish are able to regulate the Zn levels in the body (Shears and Fletcher 1983; Spry et al. 1988; Wicklund Glynn 1991). In Zn-exposed minnows, Zn levels increased two to three times in the gills and kidney after 142 d of exposure whereas the levels in the liver were not markedly influenced. These observations indicate that the Zn regulation is more precise in the liver than in the gills and kidney.

Conclusions

Zn increases the turnover rate of Cd, and Cd influences the Zn metabolism in juvenile minnows. However, these effects do not alter the toxicity of the metals, which act additively on the mortality of the fish exposed to the metal mixture. Moreover, the involvement of MT in the modulation of chronic metal toxicity is not supported by the results because induction of MT in the kidney of the exposed fish does not appear to influence mortality.

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Bioaccumulation of PCBs from Sediments by Oligochaetes and Fishes: Comparison of Laboratory and Field Studies

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Ankley, G. T., P. M. Cook, A. R. Carlson, D. J. Call, J. A. Swenson, H. F. Corcoran, and R. A. Hoke. 1992. Bioaccumulation of PCBs from sediments by oligochaetes and fishes: comparison of laboratory and field studies. Can. J. Fish. Aquat. Sci. 49: 2080–2085.

Fathead minnows (*Pimephales promelas*) and oligochaetes (*Lumbriculus variegatus*) were exposed in the laboratory to sediment samples from the lower Fox River/Green Bay, and their bioaccumulation of PCBs was compared with PCB concentrations in synoptic collections of fish (black bullhead, *Ameiurus melas*) and oligochaetes (primarily *Limnodrilus* sp.) from the field. Total PCBs and PCB homologues (expressed as lipid-normalized tissue concentrations/organic carbon-normalized sediment concentrations) were qualitatively and quantitatively similar in the laboratory-exposed and field-collected oligochaetes. PCB concentrations in *A. melas* generally were greater than in any of the other test species, due possibly to differences in exposure (e.g. biomagnification) compared with the other organisms. PCB concentrations in *P. promelas* were consistently smaller than in any of the other species investigated. These results indicate that, under the exposure regime used in this study, laboratory tests with *L. variegatus* can provide a reasonable quantitative estimate of the bioaccumulation of PCBs in field populations of oligochaetes. However, the use of *P. promelas* in laboratory sediment tests may result in significant underprediction of the exposure of indigenous benthic invertebrates and fishes to bioaccumulable contaminants.

Des tête-de-boule (*Pimephales promelas*) et des oligochètes (*Lumbriculus variegatus*) ont été exposés en laboratoire à des échantillons de sédiments provenant du tronçon aval de la rivière Fox et de la baie Green, afin qu'on puisse comparer l'accumulation des BPC dans les tissus de ces sujets à la concentration en BPC trouvées chez des sujets de collections synoptiques de poissons (barbotte noire, *Ameiurus melas*) et d'oligochètes (principalement *Limnodrilus* sp.) constituées par des prélèvements sur le terrain. Les BPC totaux et les homologues des BPC (concentrations en fonction des lipides dans les tissus et en fonction des composés organiques dans les sédiments) étaient semblables sur le plan qualitatif comme sur le plan quantitatif chez les oligochètes exposés au laboratoire et ceux prélevés sur le terrain. En général, la concentration des BPC chez *A. melas* était supérieure à celle de toute autre espèce d'expérience, peut-être à cause d'une exposition différente (p.ex. bioamplification), à comparer aux autres organismes. La concentration en BPC chez *P. promelas* était constamment inférieure à celle de toute autre espèce étudiée. Ces résultats indiquent que, dans les conditions d'exposition qui ont servi à la tenue de la présente étude, les essais sur *L. variegatus* en laboratoire peuvent donner une estimation quantitative raisonnable de la bioaccumulation des BPC chez des populations d'oligochètes observés sur le terrain. Toutefois, le recours à *P. promelas* dans les essais au laboratoire avec des sédiments, peut conduire à une importante sous-évaluation de l'exposition potentielle d'invertébrés benthiques et de poissons indigènes à des contaminants bioaccumulables.

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Determination of the potential bioaccumulation of sediment-associated contaminants by aquatic organisms is a critical component of the exposure assessment process. Due to their relative simplicity and potential for standardization of methods, laboratory exposures of aquatic organisms to field-collected sediments often are used to assess contaminant bioaccumulation. Although results of laboratory bioaccumulation tests have been used routinely in regulatory decision-making concerning contaminated sediments (e.g. dredged material disposal; U.S. Environmental Protection Agency/U.S. Army Corps of Engineers 1991), many of the tests used have not been evaluated relative to their ability to predict residue concentrations in indigenous organisms. This lack of field validation represents a potentially serious uncertainty in the assessment of bioaccumulable contaminants in sediments, and thereby hinders the implementation of standardized bioaccumulation tests.

Many different species have been used in bioaccumulation tests with sediments in the laboratory. Organisms used to assess bioaccumulation of contaminants from freshwater sediments, for example, include fishes, larval insects, and oligochaetes

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(Muir et al. 1982; Oliver 1984; Landrum and Poore 1988; Krantzberg 1989; Mac et al. 1990; Schuytema et al. 1990). In selecting appropriate organisms and exposure regimes for the development of standardized sediment bioaccumulation tests, a number of key factors must be considered. To ensure a realistic exposure, the laboratory test species should reflect the ecological position of the species of concern in the field, e.g. it would be inappropriate to test pelagic organisms to predict exposure of benthic species. In addition to representing a reasonable exposure model, the test species selected should be healthy, readily available throughout the year, and have a relatively well-defined exposure history. All of these factors are easily controlled when laboratory-cultured, rather than field-collected, organisms are used. Thus, animals that cannot be cultured, such as mayflies (e.g. *Hexagenia limbata*), may be problematical if required for routine bioaccumulation tests. Also, test species must be large enough to ensure adequate biomass (with a logistically reasonable number of organisms) for residue analyses. Therefore, the amphipod *Hyalella azteca*, although useful for evaluating the toxicity of contaminated sediments (Nebeker et al. 1984; Borgmann et al. 1989; Ingersoll and Nelson 1990), is not particularly well suited for bioaccumulation tests in which relatively low detection limits are required. Species used for sediment bioaccumulation tests also must be amenable to the long-term exposures sometimes required to achieve equilibrium concentrations of very nonpolar organic compounds. Therefore, organisms with relatively rapid life cycles, such as chironomids, are not appropriate for bioaccumulation tests with these types of contaminants.

Certain oligochaete species appear to satisfy the criteria discussed above for the development of standardized bioaccumulation tests for freshwater sediments. Oligochaetes that have been used in laboratory toxicity or bioaccumulation tests include *Stylodrilus heringianus* (Keilty et al. 1988), *Limnodrilus hoffmeisteri* (Chapman et al. 1982; Wiederholm et al. 1987; Keilty et al. 1988), *Tubifex tubifex* (Chapman et al. 1982; Wiederholm et al. 1987; Reynoldson et al. 1991), *Pristina leidyi* (Smith et al. 1991), and *Lumbriculus variegatus* (Bailey and Liu 1980; Ewell et al. 1986; Schuytema et al. 1990; Ankley et al. 1991a, 1991b; Carlson et al. 1991). We have chosen *L. variegatus* to assess the bioaccumulation of sediment-associated contaminants for a number of reasons including (a) ease of culture and handling, (b) tolerance of a wide range of sediment physicochemical characteristics (e.g. particle size, organic carbon content), and (c) adaptability to long-term (e.g. 30 d) test exposures (Phipps et al. 1993).

Herein we present the results of field validation studies conducted as part of the development of a sediment bioaccumulation test for *L. variegatus*. Specifically, to validate the test, we compared bioaccumulation of PCBs by oligochaetes exposed to sediments in the laboratory with PCB residues in synoptic collections of oligochaetes from the field. In addition, because the fathead minnow (*Pimephales promelas*) has been recommended for use in assessing the bioaccumulation of sediment-associated contaminants (Mac et al. 1990), we compared the bioaccumulation of PCBs by fathead minnows in the laboratory with PCB concentrations in the oligochaetes and in field-collected fish (black bullhead, *Ameiurus melas*, previous *Ictalurus melas*).

Materials and Methods

Sample Collection

The data analyzed herein are from a larger study conducted by the U.S. Environmental Protection Agency (EPA) which focused upon potential impacts of contaminated sediments on the lower Fox River/Green Bay, Wisconsin, ecosystem (Ankley et al. 1992). Sediments and organisms were collected in spring and summer of 1988 from 10 sites in the 11.5-km stretch of the lower Fox River below the DePere Dam and from two sites within Green Bay proper (Call et al. 1991). Sediments were collected with an Ekman dredge, homogenized, and stored at 4°C until used in laboratory exposures, within 4 mo.

Benthic macroinvertebrates were collected from the study sites using a large pump to "vacuum up" bottom material which subsequently was passed through a 500-μm-mesh sieve. Samples were stored on ice in river water until they were sorted into broad taxonomic groups (i.e. oligochaetes, chironomids), generally within 48 h. The benthos were carefully rinsed and frozen until extraction for residue analysis. Oligochaetes in the samples consisted predominantly of *L. hoffermeisteri* and *L. cervix* (Call et al. 1991). An adequate biomass of oligochaetes for residue analysis (~2 g) was collected from four of the 12 study sites.

Black bullheads for residue analysis were collected by electrofishing and/or trap nets from six of the study sites (Johnson et al. 1993). Three to five fish were composited per site for determination of PCB concentrations. Homogenates of the fish were stored frozen until extracted for analysis.

Laboratory exposures were conducted in 21-L glass aquaria containing 3 L of sediment and 6 L of hard reconstituted water (180–200 mg/L as $CaCO_3$; U.S. Environmental Protection Agency 1985). Initial toxicity tests with both solid-phase sediments and sediment pore water from the lower Fox River indicated a significant amount of toxicity to several species due to ammonia (Ankley et al. 1990; Call et al. 1991; Hoke et al. 1992), so the sediments in the bioaccumulation exposures were lightly aerated for 10 d before test initiation to allow nitrification to decrease the ammonia to nontoxic concentrations. All organisms used in the exposures came from cultures maintained at the University of Wisconsin-Superior Aquatic Toxicology Laboratory. Tests were initiated, in triplicate, with 200 adult *L. variegatus* or 45 fathead minnow fry (4–6 d old) per replicate. It should be noted that the 4- to 6-d-old fish used in our study were smaller than the 1-g fathead minnows recommended by Mac et al. (1990) for sediment bioaccumulation testing. Static exposures with the two species were conducted at 20°C for 30 d. The fathead minnows were fed newly hatched brine shrimp daily and the *L. variegatus* were fed 1.6 g of trout chow weekly. (Note that Phipps et al. (1993) do not recommend feeding *L. variegatus* when they are used in sediment bioaccumulation tests; however, the amount of food utilized in the present study would result only in minimal changes in sediment organic carbon content due to the relatively large sediment volume and initially high organic carbon concentrations.) At test termination the organisms were collected by sieving, transferred to clean water without sediment for 24 h to allow for gut clearance, and the triplicate samples pooled and frozen until extracted for residue analysis.

Chemical Analysis

Tissue samples (generally 2–10 g) were mixed with anhydrous sodium sulfate prior to extraction overnight in a Soxhlet apparatus with about 300 mL of hexane – methylene chloride (1:1, v/v). Dried sediment samples (10 g) were first extracted with acetone, followed by overnight extraction in a Soxhlet apparatus with 300 mL of methanol–toluene (3:1, v/v). The acetone and methanol–toluene fraction were then combined. The resulting tissue or sediment extracts were concentrated in a Kuderna-Danish concentrator, placed on a column of 10% deactivated alumina (Al_2O_3), and eluted with hexane to remove particulate matter. Sediment samples were then subjected to the normal phase high pressure liquid chromatography (HPLC) step described below, while lipid in the tissue samples was first removed by gel permeation chromatography (GPC). Tissue extracts (in hexane) were subjected to GPC using an HPLC system with a mobile phase of hexane – methylene chloride (9:1, v/v). The initial lipid-containing fractions were collected, taken to dryness, and lipid content determined gravimetrically. Lipid concentrations (on a wet weight basis) used for the bioavailability calculations described below were 1.05% for *L. variegatus* and field oligochaetes, 3.04% for *P. promelas*, and 1.65% for *A. melas* (Call et al. 1991). Later fractions containing the analytes were collected, recombined, and concentrated. The sediment or tissue extracts were placed on a normal phase cyanopropyl HPLC column and a solvent gradient from 100% hexane to 100% methylene chloride was used to elute the column. This resulted in a series of fractions of increasing polarity, with the initial fractions containing PCBs and subsequent fractions containing organochlorine pesticides and polycyclic aromatic hydrocarbons.

PCBs were analyzed on a Hewlett-Packard model 5880A gas chromatograph equipped with a Ni^{63} electron capture detector, a 60-m DB-5 capillary column, and a Hewlett-Packard model 7672A autosampler. A temperature-programmed run, starting at 90°C and ending at 280°C, was made as follows: 10°/min for 6 min to 150°C, 1°/min for 130 min to 280°C, and a final dwell time of 14 min at 280°C. Individual congener identification and quantification was performed with the Perkin Elmer Nelson Turbochrome II software package. The PCB standard consisted of a mixture of Aroclor 1232 – Aroclor 1248 – Aroclor 1262 (25:18:18; v/v). PCB congeners 30 and 204 (IUPAC numbering system) served as internal standards, while PCBs 65 and 166 served as surrogates for recovery determination. Recovery-corrected concentrations of total PCBs and PCB homologues were calculated by summing congener concentrations as described elsewhere (U.S. Environmental Protection Agency 1988).

Carbonate-corrected total organic carbon (TOC) concentration in the sediments was measured using a combustion technique with a Dohrmann DC183 organic carbon analyzer; the mean organic carbon concentration in the 12 test sediments was 4.54% (Ankley et al. 1992).

Data Analysis

To simplify analysis and presentation, congener-specific data were converted to concentrations of PCB homologues or total PCBs. Due to variable interferences, the monochloro homologue series was not included in our analysis. The null hypothesis, that bioaccumulation of PCB homologues or total PCBs did not vary among the test species, was evaluated using one-way ANOVA followed by Duncan's multiple range test. In this study design, there were two potential sources of variation with regard to lipid-normalized concentrations of PCBs in the test organisms: species and PCB exposure. Variations in PCB exposure among the study sites were related to the differential bioavailability of PCBs in the different sediment samples, which was due to site-specific differences in TOC concentrations. Therefore, to reduce PCB exposure variability due to site and to facilitate examination of interspecies bioaccumulation differences, we converted the tissue residue concentrations to biota-sediment accumulation factors (BSAFs)[2] before statistical comparisons were made. BSAFs were calculated by dividing lipid-normalized PCB concentrations in the test organisms by organic carbon-normalized PCB concentrations in the sediment samples, which is a relatively common approach for expressing sediment bioaccumulation data (Kuehl et al. 1987; Clarke et al. 1988; Ferraro et al. 1990, 1991; Lake et al. 1990; Brannon et al. 1991).

Results

The trichloro PCB congeners constituted the predominant homologue group in the lower Fox River/Green Bay sediments, while the tetrachloro congeners were the predominant PCBs in the test species (Table 1). Although the test organisms all exhibited detectable concentrations of the dichloro through decachloro homologues, the majority of the PCBs (generally >80%) consisted of the trichloro through hexachloro congeners (Table 1).

BSAFs for the four test species (Table 2) varied less among sites than the alternative biota-sediment factors not utilizing TOC-normalized sediment PCB concentrations (Call et al. 1991). Thus, the removal of bioaccumulation variability due to site variation in sediment TOC resulted in BSAFs being appropriate indicators of differences in PCB bioaccumulation for the species studied.

PCB homologue patterns and concentrations in *L. variegatus* and the field oligochaetes were similar to each other and to PCB patterns and concentrations in the sediments (i.e. BSAFs were close to 1; Table 2). There was a tendency, however, for the field-collected oligochaetes to have slightly higher BSAFs than the laboratory oligochaetes for PCBs with greater degrees of chlorination, i.e. the heptachloro through decachloro homologues (Table 2).

BSAFs for the total and tetrachloro through decachloro homologue concentrations of PCBs were consistently greatest in the *A. melas* samples (Table 2). In the case of the dichloro and trichloro homologues, BSAF values were either similar or lower in *A. melas* than in the oligochaetes. BSAFs for total PCBs and the nine PCB homologues always were lower (in some cases significantly so) in *P. promelas* than BSAFs in *L. variegatus*, the field oligochaetes, or *A. melas* (Table 2). However, the general homologue pattern present in the *P. promelas* samples was consistent with that seen in the other three species (Tables 1 and 2).

Discussion

We have demonstrated that laboratory exposures of *L. variegatus* to contaminated sediments resulted in relatively accurate predictions of concentrations of total PCBs and PCB homologues in field-collected oligochaetes. Although we did not evaluate the bioaccumulation of contaminants other than PCBs, it might be predicted that other persistent nonpolar organics with relatively high log K_{ow} (octanol–water partition coefficient) values would behave similarly (Veith et al. 1979). The best correspondence between the laboratory and field oligochaetes was for PCB homologues with six chlorines or less;

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[2] The sediment-based bioaccumulation factor has been inconsistently named in recent years: the bioavailability index (BI) (Kuehl et al. 1987), the accumulation factor (AF) (Lake et al. 1990), and the biota-sediment factor (BSF) (Thomann et al. 1992) are examples. Since all of these terms are quantitatively identical, we suggest the universal usage of a new, more descriptive term, the biota-sediment accumulation factor (BSAF). The BSAF is, by title and abbreviation, most analogous to the commonly used water-based bioaccumulation factor (BAF).

TABLE 1. Concentrations of PCB homologues and total PCBs in sediments from the lower Fox River/Green Bay and in organisms exposed to the sediments in the laboratory (*L. variegatus*, *P. promelas*) or collected from the field (oligochaetes, *A. melas*). Data are given as mean (± standard deviation).

	PCB concentrations				
Homologue	Sediment (ng/g OC)	*L. variegatus* (ng/g lipid)	Field oligochaetes (ng/g lipid)	*P. promelas* (ng/g lipid)	*A. melas* (ng/g lipid)
Dichloro	3532 (±2059)	593.0 (±515.0)	4806 (±7731)	101.0 (±32.07)	1753 (±3430)
Trichloro	17170 (±9275)	7857 (±5796)	10210 (±5227)	1612 (±1050)	16230 (±21900)
Tetrachloro	12600 (±6292)	15870 (±10970)	12900 (±2403)	5583 (±2966)	26910 (±11680)
Pentachloro	4328 (±2271)	5006 (±2533)	4748 (±1191)	2682 (±1055)	12970 (±3590)
Hexachloro	2221 (±1131)	2017 (±746)	3855 (±1911)	918.8 (±272.6)	7326 (±1984)
Heptachloro	977.0 (±403.0)	867.1 (±316.7)	2213 (±934.0)	461.8 (±136.2)	3745 (±732.0)
Octachloro	430.1 (±141.5)	355.6 (±91.3)	792.9 (±151.8)	213.6 (±63.9)	1515 (±303.0)
Nonachloro	74.87 (±29.27)	54.58 (±13.88)	88.30 (±21.20)	41.17 (±18.93)	198.7 (±48.5)
Decachloro	30.07 (±8.61)	15.75 (±4.00)	28.6 (±16.20)	8.33 (±3.77)	57.37 (±14.01)
Total PCBs	41450 (±19660)	32950 (±20200)	35890 (±8026)	11490 (±5464)	70900 (±41560)

conversely, the field oligochaetes tended to have slightly higher concentrations of the heptachloro through decachloro congeners than *L. variegatus*. If it is assumed that the field oligochaetes were at a thermodynamic equilibrium, this suggests that laboratory exposures longer than 30 d may be required to ensure that equilibrium concentrations of superhydrophobic chemicals are achieved by *L. variegatus*. However, *L. variegatus* can be used in longer term tests (e.g. we have conducted exposures for up to 60 d), so if test chemicals of concern have log K_{ow} values greater than 7.0–8.0 (approximate range for heptachloro PCB congeners), exposure time could be extended for the oligochaetes.

Other researchers have evaluated the relative accumulation of contaminants from sediments by aquatic organisms using ratios calculated in the same manner as the BSAF (Clarke et al. 1988; Ferraro et al. 1990, 1991; Lake et al. 1990; Brannon et al. 1991). Values reported in those studies for a variety of nonpolar organic compounds, including PCBs, generally range from around 1 to 4, which is consistent with our observations in the oligochaetes and *A. melas* and with the concept of a fugacity-based partitioning model (MacKay 1979; MacKay and Paterson 1981). In the present study, *A. melas* BSAFs for total PCBs and most of the PCB homologues were greater than respective BSAFs for either group of oligochaetes. This may reflect either biomagnification of PCBs in the fish or the exposure of *A. melas* to food and water containing PCB concentrations not reflective of sediments at the site from which the fish were collected. Interpretation of site-specific sediment BSAFs for mobile organisms, such as fishes, is far more difficult than for relatively sessile species such as oligochaetes. Even though bullhead species are not as wide-ranging as some other fish species, it nonetheless is difficult to ascertain their actual exposure in the field.

The fact that BSAFs for oligochaetes from the laboratory and the field were relatively close to 1 for most of the PCB homologue groups suggests that these species possess only a limited ability to metabolize (and excrete) this class of compounds. This limited capacity for the metabolism of nonpolar organic compounds is consistent with general observations made on other aquatic invertebrates (James 1989 and references therein). Although total PCBs were significantly greater in *A. melas* than in the field or laboratory oligochaetes, concentrations of the dichloro and trichloro homologues were the same or lower in the fish than in the worms. If the bullheads and oligochaetes were exposed to a similar mixture of PCBs in water and food, this indicates that *A. melas* possess a reasonable capacity for metabolizing and excreting the lesser-chlorinated congeners. This observation also is consistent with the results of others evaluating the metabolism and excretion of PCBs by fishes (Bruggeman et al. 1981; Niimi and Oliver 1983).

Bioaccumulation of PCBs by *P. promelas* in 30-d laboratory exposures to the test sediments was consistently less than that seen in the other groups of organisms. This observation was not particularly surprising. The fact that concentrations of PCBs in the fathead minnow were lower than in the laboratory or field oligochaetes was probably due to the different routes of exposure for pelagic versus benthic species. While benthic organisms are potentially exposed to contaminants via interstitial water, ingestion of contaminated particulate matter, and direct contact with sediments, exposure of pelagic species is limited to those contaminants that are transferred from the sediments into the overlying water and pelagic food chain and (perhaps) the ingestion of contaminated sediment. BSAFs for total PCBs and PCB homologues in *P. promelas* also were lower than corresponding values for *A. melas*. This was probably due to two factors: (a) lack of exposure via contaminated food in the lab-

TABLE 2. Average biota-sediment accumulation factors (BSAFs) for PCB homologues and total PCBs in *L. variegatus* and *P. promelas* exposed to lower Fox River/Green Bay sediments in the laboratory and in field-collected oligochaetes and *A. melas*. BSAFs are defined as lipid-normalized concentrations of PCBs in the organisms divided by organic carbon-normalized PCB concentrations in the sediment samples. Data are given as mean (± standard deviation). Values with different superscript letters within a given row (homologue series) differed significantly ($p < 0.05$).

	BSAFs			
Homologue	*L. variegatus*	Field oligochaetes	*P. promelas*	*A. melas*
Dichloro	0.21^{a} (±0.17)	2.59^{b} (±4.69)	0.04^{a} (±0.03)	0.30^{a} (±0.37)
Trichloro	0.51^{a,b} (±0.33)	0.71^{a} (±0.51)	0.11^{b} (±0.07)	0.83^{a} (±0.68)
Tetrachloro	1.35^{a} (±0.71)	1.10^{a} (±0.56)	0.50^{a} (±0.25)	2.92^{b} (±3.14)
Pentachloro	1.30^{a} (±0.62)	0.91^{a} (±0.27)	0.73^{a} (±0.32)	4.00^{b} (±2.79)
Hexachloro	1.03^{a} (±0.46)	1.42^{a} (±0.53)	0.48^{b} (±0.18)	3.37^{c} (±0.59)
Heptachloro	0.98^{a} (±0.41)	2.15^{b} (±0.79)	0.54^{a} (±0.21)	3.59^{c} (±0.92)
Octachloro	0.93^{a} (±0.39)	1.56^{b} (±0.24)	0.54^{a} (±0.17)	3.51^{c} (±0.90)
Nonachloro	0.82^{a,b} (±0.34)	1.25^{a} (±0.38)	0.58^{a,b} (±0.25)	2.54^{c} (±1.03)
Decachloro	0.57^{a} (±0.20)	0.79^{a} (±0.36)	0.27^{a} (±0.11)	2.26^{b} (±1.36)
Total PCBs	0.84^{a} (±0.35)	0.87^{a} (±0.38)	0.31^{a} (±0.14)	1.91^{b} (±1.44)

oratory and (b) insufficient time for PCB residues in fish to reach steady-state in a laboratory test. Regardless of the exact explanations for the consistently low BSAFs in *P. promelas* relative to the other groups of organisms, our data do clearly indicate that short-term exposures (i.e. ≤30 d) of pelagic fishes to solid-phase sediments in the laboratory, without food exposure, will probably result in underestimates of bioavailability of contaminants, such as PCBs, to indigenous populations either of benthic organisms or fish species. Our results also highlight the importance of field validation for any test species/exposure regime before attempting quantitative estimates of exposure for the purposes of ecological risk assessment.

In summary, this study indicates that it is possible to predict exposure of field populations of oligochaetes to PCBs through laboratory tests with *L. variegatus*. Further, our data indicate that, at least under the test regime used in the present study, the use of a model based upon *P. promelas* to predict bioaccumulation of PCBs from sediments could result in significant underprediction of exposure of indigenous species.

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Orientation and Distribution of Individual *Placopecten magellanicus* (Gmelin) in Two Natural Populations with Differing Production

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Spatial distribution patterns and orientation of individual scallops were determined for two natural populations of the sea scallop *Placopecten magellanicus* (Gmelin) from shallow coastal habitats in Newfoundland. The orientation of each scallop's dorsal–ventral axis and the positions of individuals relative to each other were determined from a composite image, constructed from a series of underwater photographs, of a grid (256 m^2) laid on the bottom at each site. Estimates of the variance to mean ratio for the number of individuals per unit area indicated that scallops from Sunnyside were aggregated, while there was evidence of a haphazard pattern at Colinet. Most scallops from Sunnyside oriented themselves with the exhalant margin facing downstream or at least some portion of the inhalant margin directed into the prevailing current whereas scallops from Colinet were randomly oriented. Differences in density, individual orientation, and patterns of spatial distribution may be partially responsible for differences in growth rates and gonad production observed between the two populations.

On a déterminé les patrons de distribution spatiale et l'orientation des individus dans deux populations naturelles de pétoncles *Placopecten magellanicus* (Gmelin) dans des habitats côtiers peu profonds de Terre-Neuve. L'orientation de l'axe dorsoventral de chaque pétoncle et la position des individus les uns par rapport aux autres ont été déterminées à partir d'une image composite, reconstruite à partir d'une série de photos sous-marines, d'une grille (256 m^2) installée sur le fond à chaque site. Les estimations de la variance par rapport au taux moyen du nombre d'individus par unité de surface ont indiqué que les pétoncles de Sunnyside étaient regroupés, tandis qu'à Colinet la distribution était aléatoire. La plupart des pétoncles de Sunnyside s'orientaient de façon à avoir la marge exhalante tournée vers l'aval, ou au moins une partie de la marge inhalante dirigée dans le courant dominant, tandis que ceux de Colinet étaient orientés de façon aléatoire. Les différences dans la densité, l'orientation individuelle et les patrons de la distribution spatiale peuvent être en partie responsables des différences dans les taux de croissance et la production des gonades observées entre les deux populations.

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A number of factors can influence the behaviour, performance, and continued survival of living organisms, including external physical factors such as temperature, salinity, and water flow and biological factors such as predation and competition (Greig-Smith 1983). Although not all of an organism's biological processes may be affected, some will fluctuate on spatial and/or temporal scales. If these factors lack a consistent influence on a species, then a random spatial distribution should arise whereas a departure from randomness would suggest that one or more environmental factors are determining its behaviour or survival (Greig-Smith 1983). There are two ways in which a spatial distribution may differ from randomness: overdispersed, with individuals aggregated (=contagious), and underdispersed, with individuals regularly spaced. The scale at which sampling is performed may significantly influence the detection of spatial patterns (Pielou 1960).

The degree of crowding to which an animal is subjected is not only a function of the population density, but also of the type of spatial distribution of the population and the size, age, or angular dispersion of each individual with its neighbours (Lloyd 1967; Weiner 1982). Processes important to survival of the species including sensory mechanisms (signals will be perceived), trophic resources (competition for food), and reproduction (fertilization success) and are not only important at high population densities but may also be important within small localized areas even at low densities (Lloyd 1967; Weiner 1982). Factors that are likely to influence spatial patterns in the marine environment are vectorial causes (i.e. physical and chemical), reproductive processes, social causes, stochastic processes, coactive processes (i.e. competition), and historical causes (Jumars and Eckman 1983).

Truly random distributions have not frequently been reported for natural populations (Riese 1979; Taylor 1984). According to Catterall and Poiner (1983), there are two principal ecological mechanisms that could cause individuals to aggregate. The first is habitat specificity which includes particular ecological or physical attributes of the habitat such as substrate type or refuge from predators. The second is intraspecific attraction where individuals have a tendency to move toward one another or are prevented from moving more than a certain distance apart. There is a delicate balance between the tendency to move closer to other individuals and thereby increase the likelihood of successful reproduction and the need to maintain a certain minimum distance from one another to reduce competition for resources and minimize trade-offs with growth and survival.

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Many species of passive suspension-feeding benthic invertebrates, including sea fans (Velimirov 1973), brachiopods (LaBarbera 1977), hydroids (Okamura 1985), and barnacles (Otway and Underwood 1987), orient themselves or their feeding appendages into local currents to enhance their filtration capabilities and exploit their food supply. Active suspension-feeders, such as *Placopecten magellanicus* (Gmelin 1791) and *Pecten maximus*, have been shown to orient their incurrent apertures into the water current in their natural habitat (Hartnoll 1967; Caddy 1968; Mathers 1976). *Placopecten magellanicus* and *Argopecten irradians concentricus* grew significantly more slowly when their inhalant openings were experimentally directed downstream than when their inhalants were facing upstream (Wildish et al. 1987; Eckman et al. 1989). Pectinids possess the ability to change orientation, possibly providing a means of maintaining good growth rates under fluctuating conditions in the natural environment (Eckman et al. 1989).

The sea scallop *P. magellanicus* supports several valuable fisheries in the northwest Atlantic, including the world's largest single natural scallop resource, the Georges Bank fishery (Caddy 1989). While there have been many studies on population density and growth rates of this species, very few investigations have considered spatial distribution. A better understanding of spatial distribution and any possible relationships between pattern and population density, growth, and total production may assist in developing programs that enhance the efficiency and management of natural fisheries or help regulate stocking density in scallop aquaculture operations (Aoyama 1989). As part of a larger project looking at the relationships between environmental conditions and scallop productivity in shallow water habitats in Newfoundland (MacDonald and Thompson 1985, 1986), the objective of this study was to determine the possible influence of density on individual orientation and distribution patterns in two scallop populations exhibiting different growth rates and production.

Materials and Methods

Conditions at Study Sites

Data on the density and spatial distribution of shallow inshore populations of scallops were collected at Colinet (47°10′N, 53°36′W) (6 m depth) and Sunnyside (47°51′N, 53°55′W) (13 m depth), Newfoundland. Neither population has in the past supported or presently supports a commercial fishery, and recreational collecting in these specific locations was infrequent. Sunnyside is a sheltered site at the western end of Bull Arm, a 6-km-long fjord-like body of water forming part of the headwaters of Trinity Bay. Colinet is a sheltered site near the mouth of the Colinet River at the northernmost part of St. Mary's Bay. Tides in eastern Newfoundland are mainly semidiurnal with a range of about 0.9 m. The wind has a prevailing westerly component during most of the year with coastal features channelling wind-driven currents and influencing the local flow of nearshore water along the coastline (Hiscock 1981; Yao 1985).

Detailed information on seasonal environmental conditions at Sunnyside and Colinet is provided in MacDonald and Thompson (1985). Briefly, there are no major rivers draining into the Sunnyside area, and salinity fluctuates between 29 and 32‰ in shallow water at both sites. At Sunnyside the temperature increased from a minimum of −1.0 to −1.5°C during February–April to a maximum of 12–14°C in September. In contrast, the temperatures in Colinet never dropped below zero in the winter and reached a maximum of 17°C in August, resulting in approximately 50% more annual day-degrees. There was a strong seasonal cycle in the quantity of suspended particulate food available at both sites. However, monthly estimates of food availability frequently revealed higher values at Sunnyside than those recorded at Colinet.

Population Growth and Production Characteristics

Detailed information on age-specific growth rates, reproductive output, and population production at Sunnyside and Colinet has been reported by MacDonald and Thompson (1986). Briefly, the shell height, soft body tissue, and reproductive output of individual scallops from Sunnyside in any given age class are greater than those of a Colinet scallop of the same age. Approximately 329 scallops were counted within 384 m^2 of bottom surveyed at Colinet resulting in a density of 0.86 individuals·m^2 whereas only 96 scallops were observed in 512 m^2 of bottom studied at Sunnyside producing a density estimate of 0.19 individuals·m^2. Despite slower growth and lower fecundity among individuals from Colinet, the greater density (approximately four times) at this site results in greater population production (59.5 versus 31.8 $kJ \cdot m^{-2} \cdot yr^{-1}$) than observed at Sunnyside. The population production is only twice the level recorded in Sunnyside despite greater densities at Colinet because the proportion of large, very fecund scallops (>13 cm) is greater at Sunnyside whereas the younger, faster growing age classes (<6 yr) are well represented at Colinet. Many studies on benthic invertebrates have reported only the production associated with somatic growth and neglected the reproductive component which can greatly underestimate total production (review by Warwick 1980).

Grid Construction

In order to estimate population density, two grids (16 m × 16 m × 2 = 512 m^2) were placed at Sunnyside and 1.5 grids (16 m × 16 m × 1.5 = 384 m^2) were placed at Colinet. To enhance visibility and reduce buoyancy, each 16 m × 16 m grid, subdivided into sixteen 4 m × 4 m sections, was constructed of white leaded rope 6 mm in diameter and then placed at a random location within a scallop bed. The grids were secured by U-shaped iron pegs hammered into the bottom over rope junctions and by concrete blocks on the corners. At 2-m intervals, 20-cm-long sections of white rope were wrapped with black plastic tape before being placed on the bottom to serve as reference points and scale bars. All shell debris and dead scallops were removed from the grids at the beginning of the observation period to ensure that scallops in the photographs were all alive. A 2-m-long iron bar (with alternating 20-cm black and white sections) was placed in the centre of each 4 m × 4 m section and a series of at least six overlapping photographs taken (Fig. 1). For logistical reasons, only one 16 m × 16 m grid placed at each site was photographed and analyzed for orientation and distribution patterns of individual scallops. Photographs were taken 2–3 m off the bottom using a Nikonos underwater camera fitted with a 28-mm lens. Enlarged black and white photographs were used to construct a composite image of the grid at each site.

The positions of individual scallops relative to reference points such as the 2-m scale bar, 20-cm strips of black tape, corners of subdivisions, and other scallops were recorded and plotted. Orientation of the dorsal–ventral axis was recorded for all scallops, unless this was not possible, as happened for a few small individuals (shell height <60 mm). Grids on the bottom were not perfectly square, so the analysis was restricted to an

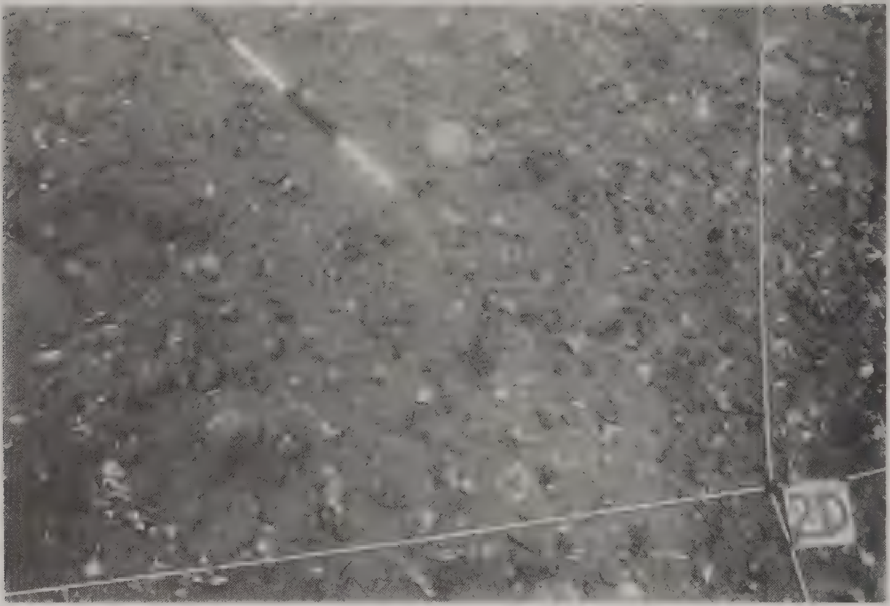

FIG. 1. Underwater photograph of *P. magellanicus* and scale bar within the experimental grid at Colinet.

exact 15 m × 15 m square centred inside the original grid at each site. This restriction slightly reduced the total number of scallops for analysis, but allowed for a more rigorous treatment of the data. To facilitate data analysis, we wish to emphasize the importance of regularly shaped study areas for anyone doing similar research. Ten different-sized scallops with known shell heights were placed beside a 2-m scale bar on the bottom in Colinet and photographed. The mean error in assigning a shell height to individual scallops in a photograph was between 1 and 7%. Scallops larger than 110 mm in shell height have a tendency to recess into the bottom and remain fairly stationary, while smaller individuals are more mobile (Caddy 1968). The presence of small mobile scallops may obscure the detection of patterns of orientation and spatial distribution. While results obtained using the entire population were reported, our central analysis focused on scallops larger than 110 mm in shell length. To allow comparison of results at each site, each scallop's location was translated as a pair of Cartesian coordinates relative to the lower left corner of the outer square and orientations translated as degrees clockwise from north.

For the analysis, the two study grids were divided into square bins of equal size ranging in number from 4 to 1024. Scallops in each bin were counted and sample mean ($\bar{x}$) and variance (s^2) calculated. If the scallops are randomly distributed, the counts should follow a Poisson distribution for which the variance to mean ratio (σ^2/μ) is 1. If they are aggregated, σ^2/μ should be greater than 1 for bins that are the same size or greater than the scale of clustering. A one-tailed test of whether σ^2/μ was significantly greater than 1 was made using the statistic

$$t = \frac{s^2/\bar{x} - 1}{(2/(n-1))^{1/2}}$$

where n is the number of bins. This statistic follows a Student t-distribution with $n - 1$ degrees of freedom (Greig-Smith 1983). The one-tailed test was chosen because our hypothesis was expressed in terms of clustering (i.e. $\sigma^2/\mu = 1$ versus $\sigma^2/\mu > 1$). While the opposite type of spatial pattern (i.e. spatial order) is conceivable, there have been no reports of such patterns in the literature. Significance was defined using $\alpha = 0.05$, and all p-values less than 0.15 were reported.

We also considered a measure of spatial crowding based on that of Lloyd (1967). Lloyd's measure "mean crowding" can be interpreted as the average number, per individual, of other individuals in the same bin. It can be expressed as

$$u^* = \mu + (\sigma^2/\mu - 1).$$

(Lloyd used m^* to denote mean crowding. Here, we used u^* to avoid confusion with m, which is used to indicate metres.) Mean crowding does not measure or indicate patterns in the spatial distribution of the scallops (i.e. clustering or ordering), but rather is a measure of the proximity of scallops to one another. Lloyd used u^* to measure the degree of spatial crowding in a bin, independent of the overall population density. To compare bins of different sizes, Lloyd defined "mean patchiness," which is u^* divided by the overall mean. Here, we adopt a similar index:

$$I = u^*/a$$

where a is the area of the bin (square metres). This new index can be interpreted as the average number, per individual, of other individuals per metre in the same bin (i.e. I is u^* standardized for bin area). Like Lloyd's mean patchiness, this new index can be used to compare bins of different sizes. It is different from Lloyd's measure in that it is standardized by a constant (i.e. the area) and not by a function of the data itself.

Note that if $\bar{x}$ and s^2 are estimates of the mean and variance of a larger population, then u^* (and therefore I) is a biased estimate of its population counterpart (Lloyd 1967). In this analysis the index I was used to compare the observed populations only and not to make inferences about larger ones. Measures of proximity, including the index I, are subject to the problems of edge effects. For scallops located in bins along the grid's outer boundary (or edge), there may have been other scallops nearby whose proximity was not measured because the scallops were outside the grid boundary. As in most studies of spatial distribution, our measures of proximity were limited to those individuals within the grid. To limit the problem of edge effects, conclusions were restricted to comparisons between the two sites, both of which shared the same geometrical layout.

There are several alternative methods for analyzing spatial distributions (see Ripley 1981 or Greig-Smith 1983 for a review). The Poisson goodness of fit test was considered, but was not feasible for small bin sizes where all counts were either 0 or 1. Two-dimensional spectral analysis was also investigated, but a much larger number of observations is required. Of the many descriptive measures that have been suggested, we ultimately chose to report the variance to mean ratio (σ^2/μ) and the index *I* because they are simple to calculate and easily interpreted in an ecological context.

Results

One hundred and fifty-seven (79%) of the 198 scallops at Colinet and 30 (81%) of the 37 scallops at Sunnyside had shell heights greater than 110 mm, and analysis was focused on this subset of larger individuals. For large scallops, there appeared to be a difference in the degree of spatial structure at the two sites (Table 1). There was strong evidence of spatial clustering at Sunnyside, where both the 4 × 4 and 16 × 16 grids yielded σ^2/μ estimates that were significantly greater than 1 ($p < 0.05$). Although this may be partially due to the multiplicity of tests, the test statistic for the 4 × 4 grid was particularly significant ($p < 0.01$) and yielded a σ^2/μ estimate of 1.98. In contrast, there was no evidence of spatial clustering at Colinet, where most σ^2/μ estimates were less than 1.

Except in the 32 × 32 grid, the index *I* indicated that the scallops at Colinet were two to three times as crowded as those at Sunnyside. Scallop densities at Sunnyside and Colinet have been reported as 0.19 and 0.86 individuals$\cdot$m^{-2}, respectively (MacDonald and Thompson 1986). Values of *I* did not vary substantially between the various bin sizes at either site, as expected given the index's standardization. The results for the 32 × 32 grids are a consequence of the bin size approaching the size of the scallops themselves.

A comparison of the locations of individual large scallops at the Sunnyside and Colinet sites in the 4 × 4 grid illustrates the apparent clustering at Sunnyside (Fig. 2). In five of the 16 bins at Sunnyside, there were no scallops whereas in another bin, there were seven. The 4 × 4 grid did not produce a similar pattern at Colinet. Despite the absence of clustering, scallops at Colinet were more crowded than those at Sunnyside.

When small scallops were included in the analysis (with the larger ones), observations at neither Sunnyside nor Colinet produced significant evidence of clustering. The 2 × 2 and 4 × 4 grids at Sunnyside yielded σ^2/μ estimates of 2.19 and 1.54, respectively, although neither was significantly greater than unity ($p > 0.05$). At Sunnyside, the inclusion of small scallops produced little change in the index *I* whereas at Colinet, the index increased by roughly 25%. After including all scallops, there was approximately four times more crowding at Colinet than at Sunnyside.

Angles of orientation were partitioned into 30° intervals (i.e. 12 groups = 360°) and each scallop assigned to a group based on the angle of orientation for the dorsal–ventral axis. It appears that most individuals at Sunnyside positioned themselves so that at least a portion of the inhalant area, or anterior and ventral margins representing an area of approximately 180°, is facing towards the direction of the prevailing westerly winds (Fig. 3). Alternatively, they could be orienting themselves to prevent the exhalant aperture from facing directly upstream. Scallops at Colinet showed no such preference. The pattern of orientation at Sunnyside was not as clearly exhibited when small scallops were included in the analysis, and there was still no evidence of a preferred orientation at Colinet.

Discussion

Many studies have suggested that the majority of species in natural benthic communities display aggregated distributions (Gage and Geekie 1973; Jumars and Eckman 1983; Vezina 1988). Ecological mechanisms that lead to aggregations are habitat specificity (based on substrate type, food resources, and refuge from predators, etc.) and intraspecific attraction, probably related to reproduction (Highsmith 1982). Improved survivorship is associated with an aggregated distribution in the ribbed mussel *Geukensia demissa*, but trade-offs include reduced food availability and slower individual growth (Bertness and Grosholz 1985). Caddy (1970) reported contagious distributions for *P. magellanicus* in the Northumberland Strait at densities ($<<5\cdot$m^{-2}) similar to those recorded in this study. While scallops from Colinet are not aggregated, spatial clustering does occur in the less dense population at Sunnyside. This is notable in that the probability of detecting a patchy distribution increases at higher densities (Pielou 1960).

Variable sediment type has also been shown to influence spatial patterns in polychaetes (Gage and Geekie 1973; Eckman 1979) and scallops, *Chlamys islandica* (Schneider et al. 1987). Greater densities of *P. magellanicus* have been recorded on sandy substrates than on muddy bottoms (Caddy 1970). Substrates at Sunnyside and Colinet both consist primarily of sand, cobble, and gravel with a few larger scattered rocks. Therefore, variation in the type of substrate between the sites is unlikely to be the cause of difference in density or distribution pattern. Caddy (1970) described contagious distributions for populations of *P. magellanicus* in commercial beds, with densities up to 4.8 adults$\cdot$m^{-2}, and for scallops at lower densities, similar

TABLE 1. Lloyd's (1967) index of crowding (*I*) standardized for bin size, and estimated variance to mean ratios (σ^2/μ) for counts of large scallops at Sunnyside and Colinet. *p*-values are from one-tailed tests of $\sigma^2/\mu > 1$ (ns: $p > 0.15$). See text for details.

Division of grid (m)	Bin size (m^2)	*n*	Sunnyside			Colinet		
			I	σ^2/μ	*p*	*I*	σ^2/μ	*p*
2 × 2	56.25	4	0.15	1.82	ns	0.69	0.30	ns
4 × 4	14.06	16	0.20	1.98	<0.01	0.69	0.89	ns
8 × 8	3.52	64	0.21	1.28	0.06	0.64	0.80	ns
16 × 16	0.88	256	0.31	1.15	0.04	0.61	0.93	ns
32 × 32	0.22	1024	<0.01	0.97	ns	0.87	1.04	ns

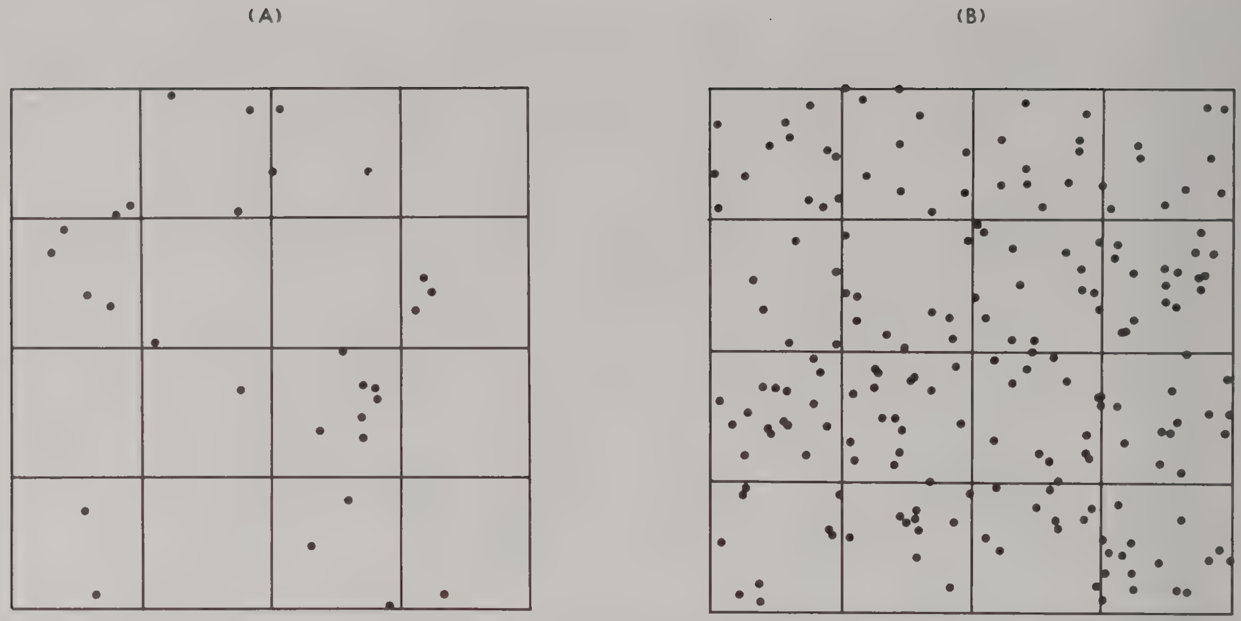

FIG. 2. Locations of large *P. magellanicus* (shell height > 110 mm) within 15 m × 15 m grids at (A) Sunnyside and (B) Colinet, Newfoundland.

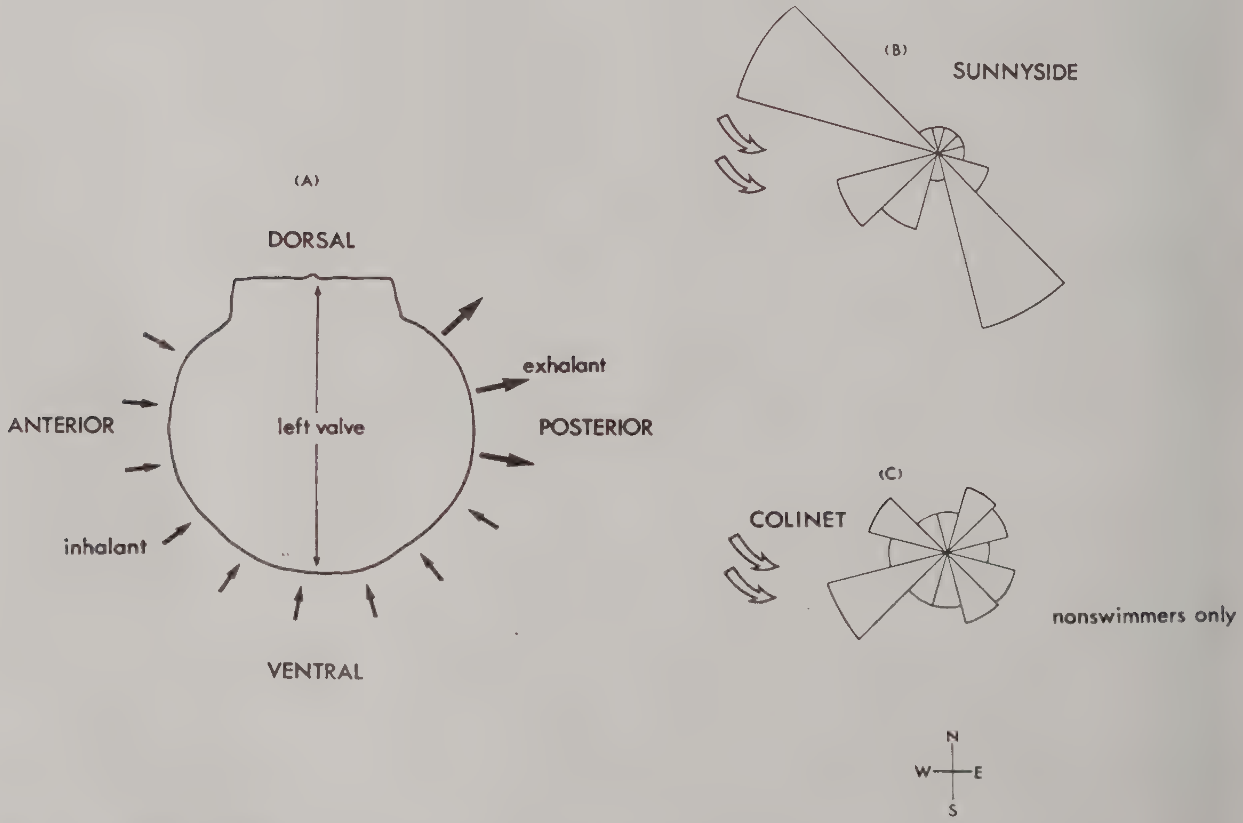
(A)
DORSAL
ANTERIOR
left valve
exhalant
POSTERIOR
inhalant
VENTRAL
(B)
SUNNYSIDE
(C)
COLINET
nonswimmers only
N
W
E
S

FIG. 3. (A) Diagram of a scallop shell showing the inhalant and exhalant margins for *P. magellanicus*. Orientation patterns of large scallops (shell height > 110 m referred to as nonswimmers) at (B) Sunnyside and (C) Colinet, Newfoundland, where westerly winds (open arrows) often dominate, are shown. The length of each 30° wedge is the percentage of scallops with their dorsal–ventral axis pointed in that direction.

to those reported for unexploited populations of giant scallops in Newfoundland ($0.19–0.86 \cdot m^{-2}$) (MacDonald and Thompson 1986). While over 60 *C. islandica*$\cdot m^{-2}$ has been reported by Vahl (1981), large pectinids are not often found at densities exceeding $10 \cdot m^{-2}$. The blue mussel *Mytilus edulis* may occur at densities high enough to deplete suspended particulate matter locally before it can be replenished during the next tidal cycle, thereby limiting its own productivity (Wildish and Kristmanson 1984; Frechette and Bourget 1985). It is possible that the greater density of scallops at Colinet ($0.86 \cdot m^{-2}$) would result in particles being removed from suspension faster than they could be replenished by advection or resuspension, thus reducing growth. If we make a major assumption that scallops are only utilizing particles in the bottom 3 cm of the water column, there would be 7.7 m^3 available for feeding in the 16×16 grid (256 m^2) at Colinet, and if the 220 scallops present had clearance rates of $10 \ L \cdot h^{-1}$, they would strip 2.2 m^3 of water every hour. Under low-flow conditions, there could be seston depletion at downstream locations in the bed. However, there is little information available on the scale on which seston depletion may be operating (Peterson and Black 1987).

Small *Crassostrea virginica* are more contagiously distributed than larger ones. Powell et al. (1987) suggested that spatial distribution patterns may change as the age structure varies because factors influencing individual survivorship and growth, including predation or competition, will change. Unlike attached species such as *C. virginica*, whose pattern of distribution is established at settlement(s) and modified by subsequent survivorship, mobile species have the capability of altering their distribution at any time. As a result of movements associated with reproductive activity, the tropical gastropods *Strombus luhuanus* and *Strombus gigas* display different types of distribution patterns depending on the proportion of adults and juveniles (Hesse 1979; Catterall and Poiner 1983). There was no significant evidence of spatial aggregation when small individuals (shell height <110 mm) at Sunnyside or Colinet were included in the respective analyses. Inclusion of small scallops at Sunnyside gave the appearance of a less aggregated distribution, possibly because they were more likely to move and randomly resettle.

The orientation of individuals has been shown to directly influence growth rates of scallops (Wildish et al. 1987; Eckman et al. 1989). Very few of the scallops at Sunnyside place their posterior or exhalant margin upstream, ensuring that exhalant openings consistently face downstream. This strongly suggests that the important factor controlling orientation is the need to prevent the exhalant aperture from facing directly upstream. An exhalant aperture that is directed into the ambient flow could cause a decrease in the volume flow rate from the animal and produce an increase in the back pressure of the bivalve pump system (Silvester and Sleigh 1984; Jørgensen et al. 1986, 1988). In turn, this would reduce the capacity of the pump (Jørgensen et al. 1988) and could negatively affect water processing functions such as suspension-feeding. Therefore, we suggest that the disadvantage of having the exhalant margin directed upstream is the controlling factor in orientation and does not explicitly require that there be an advantage to having the inhalant margin directed into the ambient flow.

Scallop growth is slower at Colinet than at Sunnyside, which has been attributed to a lower food supply of seston at the former site (MacDonald and Thompson 1985). Faster growth rates at Sunnyside may also be related to lower density (less competition for food resources) or to their consistent orientation with current direction allowing them to enhance filtration efficiency and growth. Colinet is a shallower (6 versus 13 m) and more estuarine site than Sunnyside, and complex interactions between winds, tidal forces, and the flow of the Colinet River may produce less consistent oceanographic conditions. In the absence of a consistent physical cue, there may be no advantage or disadvantage to a particular position, resulting in the lack of preferred orientation observed among individuals at Colinet.

Short-term changes in local physical conditions may have a significant influence on population spatial distribution and behaviour. Juvenile *P. magellanicus* (25–40 mm shell height) held on sandy bottoms in experimental tanks typically display aggregated distributions when inflowing seawater is in adequate supply, but when the water supply is stopped, scallops disperse, possibly in response to food shortage (M. Frechette, Department of Fisheries and Oceans, Mont-Joli, Que., G5H 3Z4, pers. comm.). When the supply of water resumes, the dispersed individuals display an aggregated pattern in less than 1 h. This behaviour is consistent with predictions that highly mobile organisms often form short-lived groups but disband when they experience negative effects (Okamura 1986). This is in contrast with longer-lived groups where continuous movement by individuals ensures the renewal of resources. At low densities the few scallops present at Sunnyside may tend to move together into local aggregations, possibly because food supply is not limiting, until they are approximately equidistant from one another. However, as density increases, these aggregations could converge to form one large group with even spacing until eventually at high densities, when attempting to space themselves out and prevent competition for resources, they may form a more random distribution.

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Top-Down Effects of Brook Trout (*Salvelinus fontinalis*) in a Boreal Forest Stream

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The impact of fish predation on epibenthic organisms at different trophic levels was studied in a series of replicated experimental outdoor channels fed by a boreal forest stream (Québec, Canada). Brook trout (*Salvelinus fontinalis*) were introduced into five of 10 channels according to a randomized block experimental design. Periphyton biomass (expressed as total chlorophyll a and total organic matter) and macroinvertebrate biomass were measured four times during the summer. The biomass of small insects such as Chironomidae was always higher in the presence than in the absence of fish, while the biomass of larger invertebrates such as *Baetis* (Ephemeroptera) and *Psychoglypha subborealis* (Trichoptera) was reduced in the presence of fish. Periphyton biomass was significantly greater in channels with fish on the first sampling date after fish introduction but not at later dates. Complementary cage experiments, involving both the inclusion and exclusion of selected invertebrates from periphyton-covered surfaces, demonstrated that the presence of *Baetis* can reduce the periphytic biomass, while the presence of *P. subborealis* can reduce the biomass of Chironomidae. Overall, these results suggest that size-selective predation by brook trout can cause profound changes in the structure of epibenthic communities at primary as well as secondary trophic levels.

L'effet de la prédation exercée par les poissons sur les organismes épibenthiques, à différents niveaux trophiques, a été étudié au moyen d'une série de canaux expérimentaux similaires, situés en plein air et alimentés par un cours d'eau d'une forêt boréale (Québec, Canada). Des Ombles de Fontaine (*Salvelinus fontinalis*) ont été placés dans cinq des 10 canaux selon un plan d'expérience prévoyant des blocs avec répartition au hasard. La biomasse du périphyton (exprimée en termes de chlorophylle *a* totale et de matière organique totale) ainsi que la biomasse des macro-invertébrés ont été mesurées à quatre reprises au cours de l'été. La biomasse des petits insectes tels que les Chironomidés était toujours supérieure en présence de poissons à ce qu'elle était en leur absence, alors que la biomasse des gros invertébrés tels que *Baetis* (Éphéméroptères) et *Psychoglypha subborealis* (Trichoptères) se trouvait réduite en présence des poissons. La biomasse du périphyton était significativement supérieure dans les canaux qui contenaient des poissons lors du premier échantillonnage qui a suivi l'introduction des poissons, mais ne l'a pas été par la suite. Des expériences complémentaires faites dans des enceintes, avec inclusion et exclusion de certains invertébrés sur des surfaces couvertes par le périphyton, ont montré que la présence de *Baetis* peut conduire à une diminution de la biomasse du périphyton, alors que la présence de *P. subborealis* peut conduire à une diminution de la biomasse des Chironomidés. Au bilan, les résultats indiquent que la prédation exercée par l'Omble de Fontaine en fonction de la taille peut conduire à de profondes modifications de la structure des communautés épibenthiques aux niveaux trophiques primaire et secondaire.

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Predation is recognized as one of the major forces structuring aquatic communities (see reviews by Sih et al. 1985 and Menge and Farrell 1989). However, in spite of an increasing number of experimental manipulations, the role of fish in structuring benthic communities in streams remains controversial. Some experiments have shown that fish predation produces little or no change in associated benthic communities (Allan 1982; Reice 1983, 1991; Flecker and Allan 1984; Culp 1986; Reice and Edwards 1986). In other cases, a significant reduction in prey density has been observed in the presence of fish (Griffiths 1981; Flecker 1984; Feltmate and Williams 1989; Gilliam and Fraser 1989; Koetsier 1989; Schlosser and Ebel 1989; Power 1990). One potential reason for this discrepancy may be that the magnitude of prey exchange (immigration/emigration), related to cage effects and drift colonization, differs considerably among experiments and has an important influence on the perceived effect of predation (Cooper et al. 1990). Alternative explanations, especially for salmonids, include the possibility that fish are weak interactors in streams (Allan 1983) or that the fish densities used in some experiments, combined with the small size of fish, have prevented the detection of significant effects (Feltmate and Williams 1989).

One aspect that has not received much attention is the vertical distribution of prey organisms within the streambed. It has been argued that refuges in the substrate may play an important role in limiting the impact of predators on invertebrates (Allan 1982; Culp 1986). In most of the above-mentioned experiments on fish predation in streams, the invertebrates inhabiting the sediment surface (epibenthos) were not considered separately from those living within the rock interstices (infauna), probably because the epibenthos usually comprises a minor part of the community as a whole (Williams and Hynes 1974). Furthermore, salmonids and other fish inhabiting stony streams may have little or no access to the animals living within rock interstices, while invertebrates that live near the sediment surface or those that drift more frequently are directly exposed to fish predation (Bisson 1978; Tippets and Moyle 1978; Grant and Noakes 1987; J. A. Bechara, G. Moreau, and L. Hare, unpubl. data). Nevertheless, despite their low contribution to total community biomass, epibenthic invertebrates can play a major role in controlling periphyton abundance and thus primary production (Lamberti and Resh 1983; Lamberti and Moore 1984; Hart 1985; Jacoby 1987; Feminella et al. 1989).

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A number of studies in lakes demonstrate that changes in populations of top predators can be transmitted to lower trophic levels through cascading trophic interactions or "top-down" effects that ultimately affect the phytoplankton (Shapiro and Wright 1984; Carpenter and Kitchell 1988; McQueen et al. 1989). These control mechanisms have also been shown to be important in streams (Power 1987, 1990). Thus, if fish are able to modify the density of epibenthic herbivorous organisms, they may indirectly affect periphyton.

We observed, during the course of experiments designed to test the effect of brook trout (*Salvelinus fontinalis*) predation on a lotic macroinvertebrate community, an increase in periphytic algae in the presence of fish. This prompted us to investigate in greater detail the impact of fish on epibenthic biota living on the stone surfaces and the role of brook trout as a top predator in cascading trophic interactions. Our hypotheses were (1) that trout either reduce or eliminate large invertebrates by selective predation and (2) that the elimination of large herbivorous insects is a major factor contributing to increased periphyton growth in the presence of fish. However, given the very low levels of phosphates in Canadian Shield streams (Parent et al. 1986), an alternative explanation to the last hypothesis may be that the presence of fish stimulates algal growth by increasing the availability of nutrients to algae through excretion and defecation. This phenomenon has been suggested for lakes (Vanni and Findlay 1990).

In this paper, we present the results of an experimental program designed to test these hypotheses. First, we analyze the overall effects of brook trout predation on the development of the epibenthic communities (invertebrates and periphyton). We then examine whether grazing or fish fertilization was responsible for the observed results by performing an enclosure/exclosure experiment.

Materials and Methods

Study Area

The experiments were carried out in Cascades Stream, a second-order tributary of the Montmorency River in the Canadian Shield. The stream flows through the Montmorency Forest, 80 km north of Québec City (47°17′N, 71°07′W). The region's climate is characterized by a mean annual temperature of 0.2°C and a total precipitation of 1500 $mm \cdot yr^{-1}$. The drainage basin lies at an altitude of 800 m and is covered by a boreal forest dominated by fir (*Abies balsamea* L.) in association with birch (*Betula papyrifera* (Marsh)). A summary of the relevant physicochemical properties of the stream during the study period is presented in Table 1.

TABLE 1. Mean and variation range of relevant physicochemical parameters of the water in the experimental channels during the study period (June–September). The number of measurements is given in brackets. Temperature was monitored continuously with a thermograph and values are 24-h averages. Conductivity, pH, and oxygen were measured every 2 wk (between 10:00 and 14:00). Nutrients were sampled monthly during the day in four of the channels.

Variable	Mean	Range
Mean temperature (°C) [65]	14.5	8.3–19.2
pH [5]	7.0	6.7–7.2
Conductivity ($\mu S \cdot cm^{-2}$) [5]	20.2	18.0–24.0
Oxygen (% saturation) [5]	116	104–130
Nitrates ($\mu g \cdot L^{-1}$) [6]	64.4	63.0–68.6
Soluble reactive phosphorus ($\mu g \cdot L^{-1}$) [7]	5.1	2.5–8.1

Experimental Design

An artificial channel system, similar to that described by Sérodes et al. (1984), was used for the experiments. This system allows the maintenance of homogeneous substrate particle size and constant water depth and velocity while preserving the natural variation in temperature, water chemistry, and drift.

Water was diverted from the middle of a beaver pool and channelled by gravity through a 20-cm-diameter pipe to a system of plasticized wooden channels, each measuring 6 m long by 40 cm wide by 40 cm high. Water was distributed by a head box equipped with an overflow pipe into five major channels, each of them divided into two, 20-cm-wide halves. We implemented a randomized block experimental design by introducing fish into one half of each major channel and leaving the other half without fish. Channels were fed continuously to maintain a constant flow velocity of 6–7 $cm \cdot s^{-1}$ and a discharge of 3.5–4.0 $L \cdot s^{-1}$. Flow velocity was within the observed range of natural stream pools in the Montmorency Forest (0–30 $cm \cdot s^{-1}$).

The bottom of each channel was completely covered with granite pebbles of uniform size (2.5–4.0 cm) contained in plastic baskets (mesh = 2.0 cm) measuring 10 × 10 × 7 cm. Unglazed ceramic tiles measuring 2 × 5 cm, placed vertically on the sides of each channel to prevent sediment accumulation, were used as substrate and sampling units for periphyton. Experiments were carried out from early June to early September 1989. The results of a preliminary experiment, performed during the summer of 1988, using the same experimental design, are also given. However, if the contrary is not specified in the text, the results presented are those obtained in 1989.

Natural colonization by drift was allowed to take place over 3 wk prior to the introduction of fish. Previous experiments in a similar experimental system showed that community densities stabilized after 2–4 wk of colonization (Sérodes et al. 1984). At the end of this period, eight trout (6.6 $ind \cdot m^{-2}$, 71.6 $g \cdot m^{-2}$) measuring between 8.0 and 12.7 cm and weighing between 5 and 21 g were introduced into five of the 10 channels. This size range, chosen to avoid cannibalism, comprises 55% of the total fish biomass in stream pools of the Montmorency Forest. Fish stocking densities were determined using the information available for the Eaux Volées Stream, located close to the Cascades Stream (R. Lacelle, Laval University, unpubl. data). A study conducted during 1988 revealed that fish densities in pools varied between 2 and 9 $ind \cdot m^{-2}$ (mean of 5 $ind \cdot m^{-2}$) and biomass between 11 and 140 $g \cdot m^{-2}$ (mean of 60 $g \cdot m^{-2}$). Fish densities in the channel system were kept higher than the mean to account for the tendency of fish to aggregate in their natural environment.

TABLE 2. Average density and dry weight (percentage composition and totals) of prey species in the stomach contents of fish from the experimental channels and the stream on the two sampling dates. Values for each invertebrate group are percentages of the total number and total dry weight (in parentheses); n = number of fish sampled; asterisks denote significant differences in total prey ingested (number and dry weight) between channel and stream fish (Mann–Whitney test; $^{**}p \leq 0.01$).

	Percentage composition number (dry weight)						Total prey	
Date/site	*Psychoglypha subborealis*	*Baetis* spp.	*Ephemerella aurivillii*	Chironomidae	Other aquatic invertebrates	Adult insects	Number (ind·fish^{-1})	Dry weight (mg·fish^{-1})
July 19								
Channels ($n = 37$)	6 (63)	10 (7)	1 (1)	37 (4)	30 (19)	16 (6)	18.7 **	(6.8) **
Stream ($n = 10$)	3 (28)	9 (20)	3 (3)	33 (4)	22 (28)	30 (17)	32.1	(10.3)
August 29								
Channels ($n = 37$)	8 (64)	12 (10)	12 (6)	41 (4)	16 (14)	11 (2)	9.7	(5.9)
Stream ($n = 10$)	1 (29)	20 (25)	1 (1)	39 (18)	25 (25)	14 (2)	9.6	(4.2)

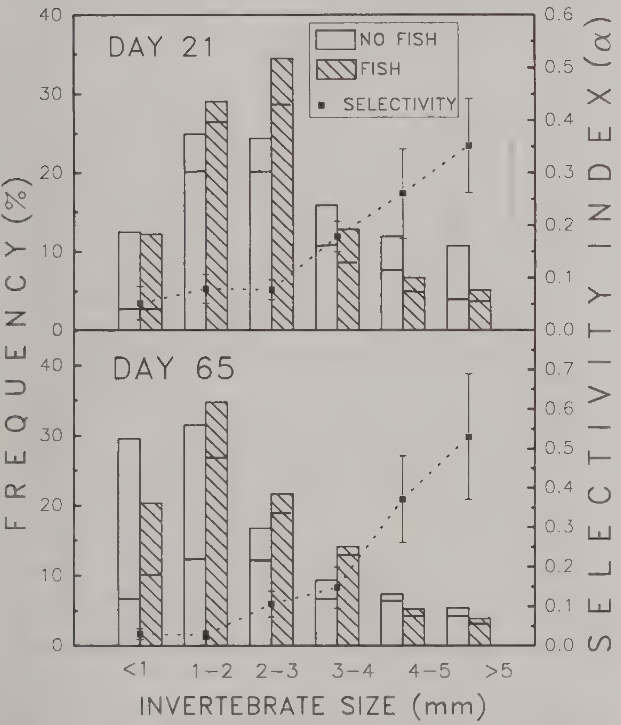

FIG. 1. Size distribution of epibenthic invertebrates in channels with and without fish (relative abundance per body length interval) and fish size selectivity 21 and 65 d after fish introduction. The lower half of each bar represents the proportion of chironomids. Random prey selection would be indicated by selectivities equal to 0.17($\alpha = 1/m$). Calculated fish selectivities (mean ± 1 SE, $n = 5$) are indicated by a broken line. Selectivity significantly varied among the different size-classes (Kruskall–Wallis test; $H = 13.28$, $p < 0.05$ for the first date and $H = 18.87$, $p < 0.01$ for the second date).

In three of the five channels, one or two fish died as a result of being trapped between two plastic baskets. Dead fish were removed as soon as detected and immediately replaced by fish previously acclimated in a similar experimental system in order to maintain densities between 5 and 6.6 ind·m^{-2}. To keep the fish within the channels, and to prevent the entry of stream fish, a 5-mm-mesh grid was placed at each end of the channels the day before the fish were introduced. In addition, the entire system was covered with mesh to prevent the trout from jumping out of the channels and to prevent predation by terrestrial vertebrates.

Sampling Program

In the 1989 experiment, six ceramic tiles were randomly sampled in each of the channels 4 d before and 21, 50, and 65 d after fish introduction. Algal biomass, as estimated by total chlorophyll *a*, was determined on three replicates by extraction in 90% acetone and subsequent absorbance readings at 665 and 750 nm. The remaining three tiles were used to estimate total organic matter by combustion in a muffle furnace at 550°C (ash-free dry weight). In the 1988 experiment, five samples were obtained from the walls of each channel (area = 5.0 cm^2) with a syringe sampler (Loeb 1981) 25 d after fish introduction.

In the 1989 experiment, random samples of epibenthic invertebrates were obtained from the walls of each channel by covering a 10 × 10 cm quadrat with a Plexiglas box. All attached organisms were then removed by siphoning the wall surface with a brush attached to a plastic tube. Samples were filtered through a 250-μm-mesh screen. Three replicate samples per channel were collected 22, 51, and 66 d after fish introduction. The density of the large trichopteran *Psychoglypha subborealis* was estimated by enumerating all the larvae crawling on the channel walls. In the preliminary 1988 experiment, five replicated samples per channel were taken from the pebble surfaces of each channel using the same technique 15 and 29 d after fish introduction. However, this sampling may be less accurate than that of 1989 because some invertebrates may have escaped the siphoning by rapidly moving into the interstitial spaces of the pebble substrate. Furthermore, light penetration and sediment deposition on the pebble substrate may have been different from the channel walls, which may limit the interpretation of the relationships between invertebrate and periphyton biomass.

Fish stomach contents were sampled by stomach flushing (Strange and Kennedy 1981) 21 and 65 d after the fish were introduced into the channels (July 19 and August 29, 1989, respectively). Samples were taken the day prior to benthic sampling between 22:00 and 23:00. Ten fish of similar size were captured simultaneously by electrofishing from a nearby pool

TABLE 3. Average biomass (mean ± 1 SE, $n = 5$) and randomized block ANOVA summary (F values) of the chlorophyll *a* and invertebrate responses in the presence and absence of fish in the 1988 experiment. Invertebrate samples were taken 15 and 29 d after fish introduction (August 3 and 17, respectively). Chlorophyll *a* was sampled 25 d after fish introduction (August 12). Significant differences are denoted with asterisks ($*0.05 \geq p > 0.01$, $***p \leq 0.001$).

	Days after fish introduction	Biomass ($mg \cdot m^{-2}$)		F values (df = 1,4)
		No fish	Fish	
Ephemeroptera				
Baetis	15	49.6 ± 12.2	16.9 ± 4.2	9.5*
	29	6.4 ± 2.9	2.9 ± 1.1	0.6
Ephemerella	15	10.9 ± 1.3	11.0 ± 1.1	0.0
	29	6.9 ± 1.3	8.9 ± 2.8	0.2
Chironomidae				
Tanypodinae	15	32.3 ± 7.8	15.9 ± 4.4	1.7
	29	8.4 ± 1.1	8.5 ± 2.4	0.1
Orthocladiinae	15	11.8 ± 2.2	10.5 ± 2.6	0.5
	29	6.9 ± 0.7	8.8 ± 0.9	4.0
Tanytarsini	15	3.2 ± 1.2	1.7 ± 0.6	0.4
	29	1.1 ± 0.3	0.9 ± 0.2	0.2
Chlorophyll *a*	25	15.1 ± 3.7	52.7 ± 8.9	20.4***

in Cascades Stream for comparison of diet composition and abundance.

Invertebrates were preserved in 4% formalin and later separated and identified to the genus or family level. All organisms were measured to the nearest 0.1 mm using a dissecting microscope fitted with a drawing tube and a digitizing tablet connected to a Sigma-Scan Scientific Measurement System®. Biomass was estimated from regression relationships that we developed, between body or head width and body weight, for each taxon (Bechara 1992).

Enclosure/Exclosure Experiments

These experiments were designed to test the hypothesis concerning the role of large invertebrates in the control of periphytic biomass. Unglazed ceramic tiles (10 × 10 cm), to be used in the enclosure/exclosure experiments, were first placed in channels without fish to allow natural colonization over 1 mo. The tiles were then exposed to two treatment categories, according to a randomized block factorial design: (1) the presence or absence of fish (''fish'' treatment) and (2) varying exposure to fish and invertebrate predation and grazing by the use of cages (''cage'' treatment). The cages used in this experiment were made of a transparent Plexiglas frame (10 × 10 × 5 cm), covered with 1.5-mm-mesh Nytex. The cage treatment had four levels. The first was isolation from large invertebrates: a tile in an empty cage. The second was exposure to trichopteran larvae: a tile with two *Pschoglypha subborealis* (13–15 mm long) in a cage. The third was exposure to Ephemeroptera nymphs: a tile with three *Baetis* spp. (6–8 mm long) or three *Ephemerella aurivillii* (5–7 mm long) in a cage. The fourth treatment, no protection from fish predation (an uncaged tile), was used as a control. The two ephemeropterans are classified as collector–gatherers and scrapers by their trophic relationships (Merritt and Cummins 1984) and the genus *Psychoglypha* as a collector–gatherer and shredder–detritivore. The tiles were placed on the bottom of all channels facing the current at an angle of 45°. There were five replicates for each treatment level.

The enclosure/exclosure experiment was first carried out in late July 1989, when *Baetis* spp. were the dominant ephemeropterans. It was repeated a second time in late August – early September 1989, when *E. aurivillii* was more abundant. The latter thus replaced *Baetis* spp. in the cage treatment. Each experiment lasted 2 wk, and during this time the Nytex cages were routinely cleaned by gentle brushing to remove sediment.

At the end of the first experiment, a periphyton subsample (5 cm^2) was obtained from each tile for chlorophyll *a* analysis. For the second experiment, a small colonized tile (2 × 5 cm), placed over the larger tile at the start of the experiment, was used as a sampling unit. In the second experiment, total organic matter was also estimated. At the end of the first experiment, all chironomids were collected from the tiles and the inside of the cages. Because chironomids colonized both the tiles and the Nytex cage, the sum of the internal surface of the cage was used to estimate biomass in milligrams of dry weight per unit area.

Data Analyses

Chlorophyll *a*, organic matter, and invertebrate biomass data were first tested for normality and homogeneity of variance using the Kolmogorov–Smirnov test and the Cochran test, respectively (Sokal and Rohlf 1981). Whenever the data did not conform to the assumptions of normality and homogeneity of variance, they were transformed using either the Box–Cox algorithm or the Box–Cox–Bartlett algorithm (Sokal and Rohlf 1981).

The normally distributed 1989 data were analyzed using a split-plot factorial ANOVA with repeated measures, with fish as the main plot and time as subplots. This test is not adjusted for autocorrelation, which is inherent in the repeated measures analysis. However, for certain correlation patterns, known as Type H covariance, the usual F tests are exact (Kirk 1982). This condition was tested by applying a sphericity test, and in all cases, the null hypothesis of type H covariance structure was accepted at $p > 0.05$. Planned, simple contrasts were performed for testing the differences between levels of fish treatment on each sampling date. The normally distributed 1988 data were analyzed using a randomized block ANOVA applied to each of the sampling dates.

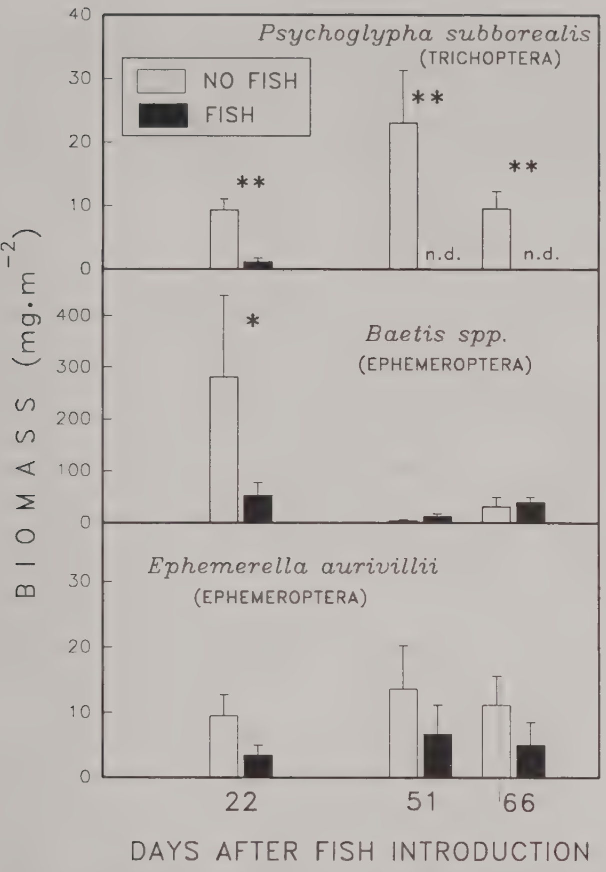

FIG. 2. Biomass (mean ± 1 SE) of the three species of epibenthic Trichoptera and Ephemeroptera in the presence and absence of fish on three sampling dates in July and August 1989. Asterisks represent significant differences between the "no fish" and "fish" treatment levels for each sampling date (*$p < 0.05$, **$p < 0.01$; Friedman test on each sampling date for *P. subborealis* and *Ephemerella* and orthogonal contrasts shown in Table 4 for *Baetis*; n.d., not detected).

Data from cage experiments were analyzed using a randomized block factorial ANOVA. Simple contrasts were also performed, involving planned comparisons among uncaged tiles with and without fish and each of the levels of the remaining treatments (12 contrasts), as well as among cages with and without fish at each level of cage treatment (eight contrasts). As these contrasts were not orthogonal, the Dunn-Šidák adjustment was applied to reduce the Type I error rate (Sokal and Rohlf 1981). On occasion, unplanned pairwise comparisons were also applied. In these cases, the least square difference test (LSD), adjusted for the Bonferroni inequality, was used ($\alpha = 0.05$ divided by the number of possible pairwise comparisons).

The transformations applied did not correct the lack of normality of certain invertebrate biomass data. Nonparametric tests (Mann–Whitney, Kruskall–Wallis, or Friedman) were performed instead for each of the sampling dates. All of the statistical analyses were performed using SAS (1985).

The Manly/Chesson index was used to estimate prey size selectivity (Chesson 1978, 1983) by comparing the relative abundance of 1-mm invertebrate size classes in fish stomach contents with that of the epibenthos on the channel walls. The following equation was applied:

$$\alpha_i = (r_i/n_i)/\sum_{j1}^{m}(r_j/n_j)$$

where $i = 1, 2, \ldots, m$ and m is the number of prey size classes, r_i is the proportion of prey of size i in the diet sample, and n_i is the proportion of prey of type i in the environment. The index varies from 0 to 1 and random selection is indicated by $\alpha_i = 1/m$. For each channel, data from all fish were pooled and compared with epibenthic size composition on each of the two sampling dates. We considered data from each channel as replicates of the index.

Results

Community Structure and Fish Selectivity

Throughout the study period, the epibenthic community of the channels was dominated by Ephemeroptera (*Baetis flavistriga* McDunnough, *Baetis bruneicolor* McDunnough, and *Ephemerella aurivillii* Bengtsson), Chironomidae (Orthocladiinae, Chironominae, and Tanypodinae), and Trichoptera (*Psychoglypha subborealis*, (Banks)). Collectively, they made up more than 90% of total invertebrate biomass above 250 μm.

These same taxa represented 48–73% (numerically) and 55–84% (by biomass) of the stomach contents from channel and stream fish (Table 2). In channel fish, chironomids tended to be numerically dominant, while the large trichopteran *P. subborealis* dominated the stomach content weight. In terms of number of individuals, the percent composition of invertebrate taxa in channel fish was similar to that of the stream fish stomach contents on the first sampling date (chi-square goodness-of-fit test, $\chi^2 = 9.4$, $p < 0.05$) but significantly different on the second ($\chi^2 = 19.1$, $p > 0.05$). The percent composition was always significantly different in terms of biomass (first date, $\chi^2 = 27.7$, $p > 0.05$; second date,

TABLE 4. Split-plot ANOVA summary (*F* values) of the invertebrate biomass responses to the main effects and interactions of the experimental treatments in the 1989 experiment. Planned orthogonal contrasts, comparing channels with and without fish, are also shown for each sampling date. Significant differences are denoted with asterisks (*$0.05 \geq p > 0.01$, **$0.01 \geq p > 0.001$, ***$p \leq 0.001$).

Dependent variable	Treatments		Interaction: fish × time (df = 2,8)	No fish – fish contrasts (df = 1,8)		
	Fish (df = 1,8)	Time (df = 2,8)		Day 22	Day 51	Day 66
Baetis	2.2	8.2**	2.1	6.4*	0.1	1.7
Orthocladiinae	60.4***	1.8	0.6	7.6*	8.8**	6.7*
Chironominae	7.5*	5.3*	3.5	0.4	18.8**	9.7**
Tanytarsini	2.6	0.5	0.2	0.3	9.5**	4.8

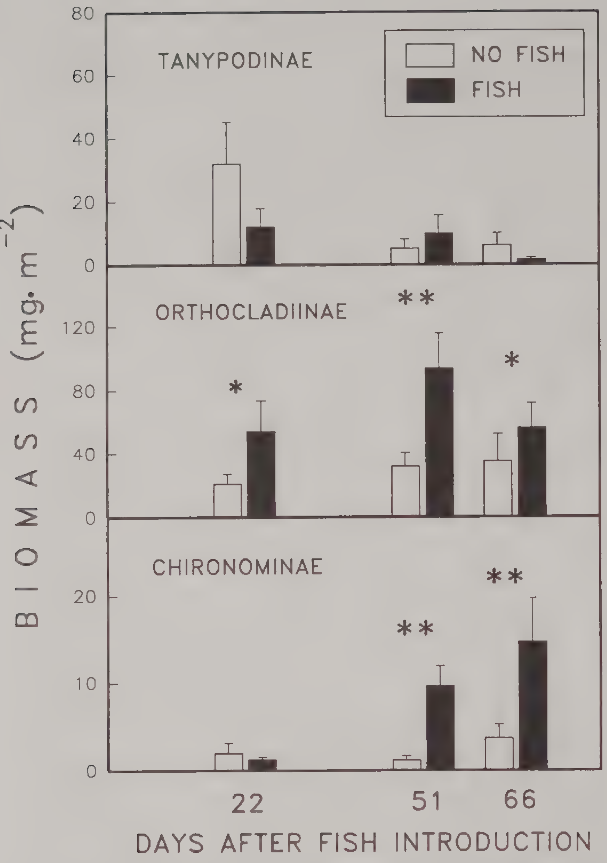

FIG. 3. Biomass (mean ± 1 SE) of epibenthic chironomid subfamilies in the presence and absence of fish on the three sampling dates after fish introduction in July and August 1989. Asterisks represent significant differences between the "no fish" and "fish" treatment levels for each sampling date ($*p < 0.05$, $**p < 0.01$; Friedman test applied for Tanypodinae and orthogonal contrasts shown in Table 4 for the other subfamilies).

$\chi^2 = 35.2$, $p > 0.05$). Moreover, stream fish ingested a sigificantly higher total number and biomass of prey than channel fish on the first sampling date but not on the second (Table 2).

The overall size structure of the epibenthic invertebrate community, estimated as the relative abundance (proportion of the total number of individuals per square metre) of each body length interval, was significantly affected by the presence of fish on the first sampling date ($\chi^2 = 11.5$, $p < 0.05$; Fig. 1) but not on the second ($\chi^2 = 10.6$, $p < 0.07$, borderline insignificance; Fig. 1). In general, benthic invertebrates larger than 4 mm were proportionally less abundant in channels with fish, with an associated increase in the proportion of small- to medium-sized animals, especially chironomids (Fig. 1). This pattern can be explained at least in part by the fact that fish exhibited a strong preference for invertebrates larger than 4 or 5 mm on both sampling dates (Fig. 1).

Changes in Benthic Insect Biomass

In the 1988 experiment, the biomass of *Baetis* was significantly lower in the presence of fish on the first sampling date. In contrast, the biomass of *Ephemerella* and of Chironomidae was not affected by the presence of fish (Table 3).

In the 1989 experiment, *P. subborealis* biomass was always significantly lower in channels with fish (Friedman test, $p < 0.05$; Fig. 2). *Baetis* biomass exhibited a significant time effect (Table 4), and orthogonal contrasts show that mean biomass values were significantly lower in the presence than in the absence of fish on the first sampling date (Table 4; Fig. 2). *Baetis* biomass declined sharply in both the presence and the absence of fish after the first sampling date (LSD test with Bonferroni adjustment, $p < 0.05$). Moreover, mean nymph size on the second sampling date was significantly lower than on the first sampling date (mean ± 1 SE, 2.2 ± 0.2 and 3.8 ± 0.2 mm, respectively; Friedman test, $p < 0.05$). In contrast, *E. aurivillii* biomass showed no significant change in the presence of fish (Friedman test, $p > 0.05$; Fig. 2).

Biomass of chironomids generally increased in the presence of fish in the 1989 experiment, with the exception of the subfamily Tanypodinae (Friedman test, $p > 0.05$; Fig. 3). Biomass of the subfamily Orthocladiinae (the more abundant chironomid taxon) was significantly higher in the presence of fish (Table 4). Orthogonal contrasts show that these differences were consistent over the study period, regardless of changes in the relative abundances of the genera contributing to the biomass of this subfamily (Table 4; Fig. 3). At the beginning of the experiment, *Cricotopus* and *Rheocricotopus* were the most abundant genera, but with time, *Orthocladius* became dominant. The Chironominae showed significant fish and time effects (Table 4; Fig. 3). Orthogonal contrasts showed significant fish effects at days 51 and 66 (Table 4; Fig. 3). Early larval stages of *Micropsectra* (tribe Tanytarsini; Table 4) and *Microtendipes* (tribe Chironomini; Friedman test, $p < 0.05$) were responsible for most of the observed responses of the subfamily Chironominae.

Changes in Periphyton Biomass

The periphyton was numerically dominated by diatoms (*Fragillaria intermedia* Grun., *Tabellaria flocculosa* (Roth), and *Achnanthes minutissima* Kütz.), blue-green algae (*Lyngbia lim-*

TABLE 5. Split-plot ANOVA summary (*F* values) of the total chlorophyll *a* and organic matter (ash-free dry weight) responses to the main effects and interactions of the experimental treatments in the 1989 experiment. Planned orthogonal contrasts, comparing channels with and without fish, are also shown for each sampling date. Significant differences are denoted with asterisks ($*0.05 \geq p > 0.01$, $**0.01 \geq p > 0.001$, $***p \leq 0.001$).

Dependent variable	Treatments		Interaction: fish × time (df = 3,12)	No fish – fish contrasts (df = 1,12)			
	Fish (df = 1,12)	Time (df = 3,12)		Day 0	Day 21	Day 50	Day 65
Chlorophyll *a*	13.3*	69.5***	8.4**	1.3	12.8**	1.4	1.4
Organic matter	2.3	32.7***	3.6*	0.8	4.8*	0.3	0.4

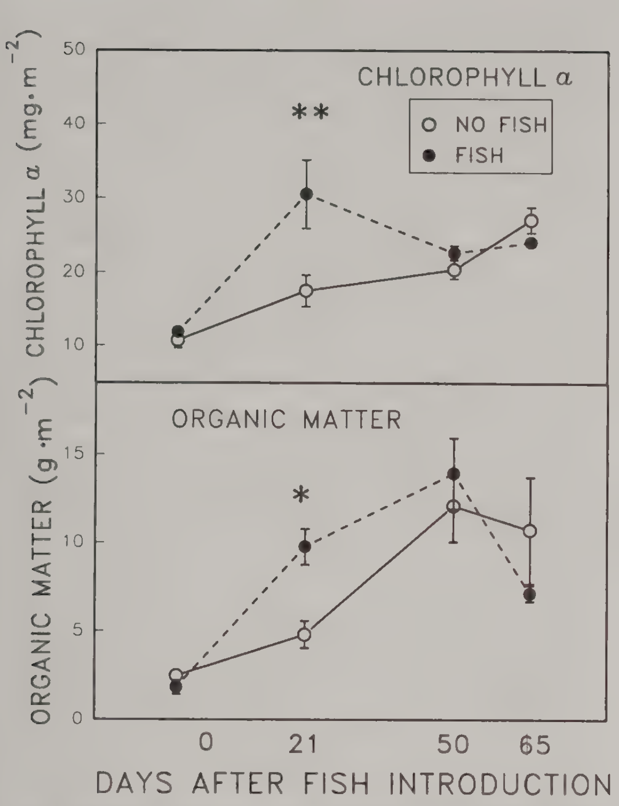

FIG. 4. Temporal changes in total chlorophyll a and organic matter (ash-free dry weight) (mean ± 1 SE) in the presence and absence of fish before and after fish introduction. Asterisks represent significant differences between the "no fish" and "fish" treatment levels for each sampling date ($*p < 0.05$, $**p < 0.01$; orthogonal contrasts shown in Table 5).

netica Lemmermann, *Oscillatoria utermoehlii* J. de Toni, and *Aphanocapsa grevillei* (Hass.)), and green algae (*Pseudendocolnium* sp. and *Gloeocystis vesiculosa* Naegeli).

In the 1988 experiment, periphyton biomass, as measured by chlorophyll a, was three times higher in the presence than in the absence of fish (Table 3).

In the 1989 experiment, total chlorophyll a and organic matter on tiles exhibited a strong fish × time interaction (Table 5). Orthogonal comparisons showed significant differences only 21 d after fish introduction, at which time the chlorophyll a values were almost 100% higher in the presence of fish (Fig. 4). This was coincident with lower *Baetis* biomass in the presence of fish (Fig. 2).

Enclosure/Exclosure Experiments

First experiment

Periphyton biomass, as measured by total chlorophyll a, was significantly affected by the cage treatment, but a fish × cage interaction was also observed (Table 6). Both in the presence and in the absence of fish, chlorophyll a values were reduced in cages with *Baetis* to the levels found on uncaged tiles in the absence of fish, values significantly lower than those found on uncaged tiles in the presence of fish (simple contrasts with Dunn–Šidák adjustments; Fig. 5). However, the periphyton biomass of empty cages and of cages with *P. subborealis* was not significantly different from that of uncaged tiles in the presence of fish (simple contrasts with Dunn-Šidák adjustments; Fig. 5).

Chironomid biomass was affected by the cage treatment but not by the fish treatment (Table 6). The presence of *P. subborealis* strongly reduced the biomass of chironomids, both in the presence and in the absence of fish, as compared with that in empty cages (LSD tests with Bonferroni adjustments; Fig. 6). In cages with *Baetis* and on uncaged tiles, intermediate chironomid biomass values were observed.

Second experiment

In contrast with the first enclosure/exclosure experiment, periphyton biomass, as measured by chlorophyll a, was not affected by the treatments (Table 6; Fig. 5). Total organic matter showed a significant fish effect (Table 6), but simple contrasts showed no significant differences among treatment levels (Fig. 7).

Discussion

Fish Predation on Benthic Insects

The preceding experiments suggest the existence of "top-down" effects in the experimental stream system, whereby trout exert a control on the structure of the epibenthic invertebrate community, which in turn can modify the biomass of periphyton.

The presence of fish affected the invertebrate community structure by decreasing the biomass of large invertebrates and increasing the small to medium size-classes, especially chironomids. Our data suggest that these effects may be

TABLE 6. Two-way ANOVA summary (F values) of cage experiments 1 and 2 (1989) for total chlorophyll a, organic matter (ash-free dry weight), and chironomid biomass (main effects and interactions). Significant differences are denoted with asterisks ($*0.05 \geq p > 0.01$, $**0.01 \geq p > 0.001$, $***p \leq 0.001$).

	Treatments		
Dependent variable	Fish (df = 1,32)	Cage (df = 3,32)	Interaction: fish × cage (df = 3,32)
Total chlorophyll a			
Experiment 1	2.57	16.73***	3.52*
Experiment 2	1.88	1.14	1.37
Chironomid biomass			
Experiment 1	2.27	39.03***	0.38
Organic matter			
Experiment 2	7.52**	0.48	2.62

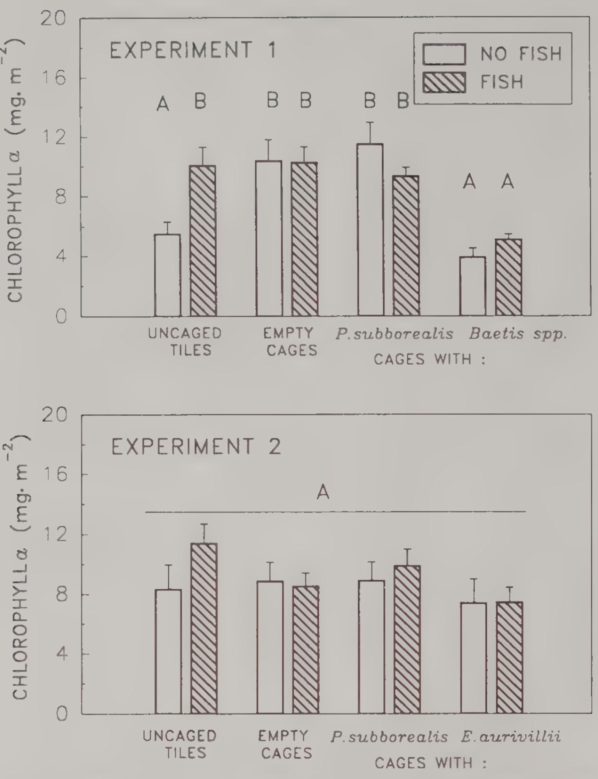

FIG. 5. Total chlorophyll *a* (mean ± 1 SE) in the first and second enclosure/exclosure experiments in the presence and absence of fish for each of the four cage treatment levels. Simple contrasts with the Dunn–Šidák adjustment were used to compare means of uncaged tiles with the remaining treatment levels. Identical letters represent no significant differences (A < B at $p < 0.003$).

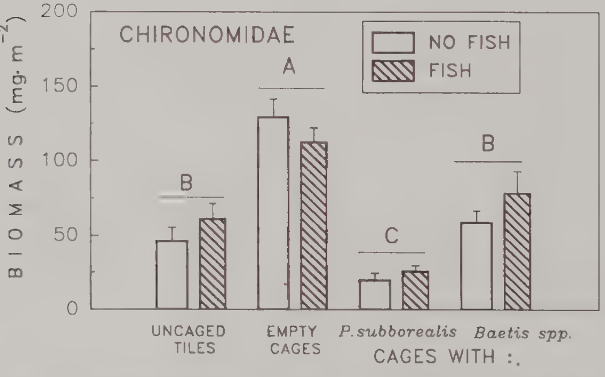

FIG. 6. Chironomid biomass (mean ± 1 SE) in the first enclosure/exclosure experiment in the presence and absence of fish for each of the four cage treatment levels. LSD tests with the Bonferroni adjustment were used to compare means of the four cage treatments. Bars with identical letters represent no significant differences (A > B > C at $p < 0.012$).

explained at least in part by the size-selective predation of trout. This increase in chironomids in the presence of fish predators had not been previously reported for streams, although Crowder and Cooper (1982) and Gilinsky (1984) had observed a similar phenomenon for benthos in lakes.

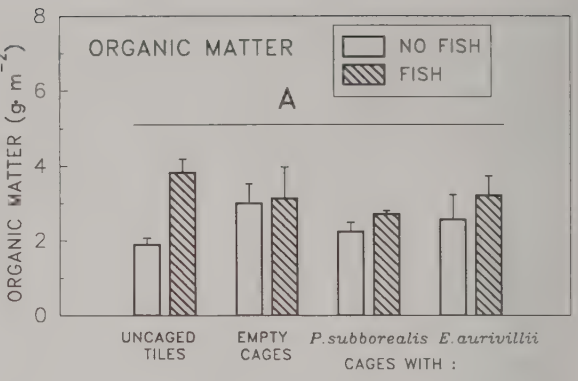

FIG. 7. Organic matter (mean ± 1 SE) in the second enclosure/exclosure experiment in the presence and absence of fish for each of the four cage treatment levels. There were no significant differences between uncaged tiles with and without fish and the remaining treatment levels (simple contrasts with the Dunn–Šidák adjustment, $p > 0.003$).

The chironomid biomass of the pebble substrate epibenthos did not increase in the 1988 experiment. However, in this same experiment, the abundance (individuals per square metre) of small Orthocladiinae and Chironomini in the epibenthos and the Orthocladiinae abundance in the pebble substrate as a whole were significantly higher in the presence than in the absence of fish (J. A. Bechara, G. Moreau, and L. Hare, unpubl. data).

A cage experiment showed that in the presence of large insects (*Baetis* and especially *P. subborealis*), chironomid biomass was strongly reduced. It can be inferred from this result that, in the presence of fish, chironomids benefitted from a reduction in large invertebrate densities induced by the size-selective predation of fish. The omnivorous regime of *P. subborealis* (Winterbourn 1971) suggests that both competition and predation may have been important in controlling chironomid abundance. To reinforce this assumption, we conducted an analysis of the stomach contents of 20 *P. subborealis* larvae. They consisted of organic detritus and algae, and 80% of them contained at least one recently ingested chironomid larva. Furthermore, in both channels and cages, this trichopteran was able to clean large surfaces of substrate, thus disrupting chironomid habitat while crawling and feeding.

Because fish stomach contents were composed of a mixed array of epibenthic and drifting invertebrates (J. A. Bechara, G. Moreau, and L. Hare, unpubl. data), size-selectivity values could be considered biased. However, in an experiment conducted during 1988 in the same channel system, the size structures of the epibenthic and drifting invertebrates were shown to be similar (J. A. Bechara, G. Moreau, and L. Hare, unpubl. data). Given that the Manly/Chesson index takes into account the relative proportion of prey types, and not changes in absolute prey densities, estimated values are valid approximations of actual fish selectivity. That *P. subborealis* was rare or absent in the epibenthos, but represented a large proportion of fish stomach biomass, is another apparently controversial result. However, because selectivity was calculated on the basis of relative abundance (number of individuals), and not relative biomass, the contribution of this trichopteran species to the total abundance of epibenthos and fish stomach contents was low. It is therefore improbable that this led to any significant distortion of the results. When we intentionally placed individuals of *P. subborealis* on the channel bottom, we noticed that they were rapidly detected and eaten by fish. Thus, individuals of this species were probably consumed as soon as they appeared in the epibenthos, which may explain their absence in the epibenthos on the two later sampling dates. In contrast, this species was not affected by fish in the pebble interstices (infauna), which seem to be an effective refuge for large invertebrates (J. A. Bechara, G. Moreau, and L. Hare, unpubl. data).

Contrary to the hypothesis put forth by Allan (1983), and the results of other experimental manipulations (Allan 1982; Flecker and Allan 1984; Culp 1986; Reice and Edwards 1986), our results suggest that salmonids are strong interactors in streams (sensu Paine 1980). There are several possible explanations for the difference between our results and those of previous investigators. Firstly, Feltmate and Williams (1989) have suggested that some of the discrepancies among trout predation studies may be attributed to the different predator densities used in each case. Working with rainbow trout (*Oncorhynchus mykiss*) at densities five times higher than that used by Allan (1982), they found a significant effect on a stonefly population. However, the densities used by Reice and Edwards (1986) and Culp (1986) were, respectively, 2 and 5–21 times higher than Allan's (1982), and they did not observe modifications of the benthos. In our study, the densities used were 15 times higher than Allan's (1982). These values may have been too high to satisfy the minimum maintenance requirements of the fish because the mean fish weight at the end of the study period was 10% lower than the stocking biomass. An alternative explanation to the low fish growth could be reduced feeding activities due to the unusually high temperatures registered during the study period (Table 1), temperatures that are considered suboptimal for brook trout (Power 1980). Furthermore, Bussières (1991) found mean values of brook trout food capture of 154 $mg \cdot m^{-2}$ (July 1988) and 161 $mg \cdot m^{-2}$ (August 1988) in the pools of a nearby stream in the Montmorency Forest (''Eaux Volées''). These values are, respectively, 4.3 and 4.5 times higher than those in the channels for the same months and sampling hours. Given that the total benthic densities of the above-mentioned stream were similar to those from the channels (Elouard 1977; Bechara 1992), these results suggest that trout did not excessively exploit the benthos in the experimental system. For these reasons, our results cannot be simply attributed to the fish densities used in the experiments. However, the results of the experiments might better reflect trophic interactions in natural stream pools, where fish tend to concentrate, then in streams as a whole.

A second possible explanation for the difference between our results and those of previous investigators is that in the above-mentioned studies, epibenthic invertebrates were lumped together with other organisms collected in the first 5–10 cm of substrate, and thus the effects on the invertebrates living at the surface may have been obscured. Although epibenthic invertebrates usually constitute a small proportion of the community, they are the most accessible to salmonid fish (J. A. Bechara, G. Moreau, and L. Hare, unpubl. data).

Lastly, Cooper et al. (1990) showed that when drift is abundant, high colonization rates tend to compensate for the effects of predation. In a literature review, the authors found that a significant impact of fish was observed in experiments where drift densities were low (3.4–5 mayfly nymphs$\cdot 100\ m^{-3}$), while, at much higher drift densities (50–1300 nymphs$\cdot 100\ m^{-3}$), fish predation effects were not detected. In our channel system, the densities of mayfly nymphs in drift were always higher than 100 ind$\cdot 100\ m^{-3}$ (J. A. Bechara, G. Moreau, and L. Hare, unpubl. data). These relatively high drift densities did not mask the impact of fish on *Baetis* on the first sampling date, but could have been responsible for the lack of fish impact on *Baetis* at later sampling dates and on *Ephemerella* biomass on all sampling dates.

The experimental system used was designed to approach natural stream conditions while at the same time maintaining constant certain possible confounding factors, such as substrate complexity, current velocity, and discharge. The benthic community that colonized the experimental system was shown to be similar to that of natural stream pools (J. A. Bechara, G. Moreau, and L. Hare, unpubl. data), which suggests that the conclusions of this study may also be valid for the pools of the Cascades Stream. Furthermore, a study conducted by Bowlby and Roff (1986) on 30 stream sites in Ontario (Canada) supports some of our findings. For example, the biomass of nonpiscivorous fish (including brook trout) was positively related to the biomass of small benthic invertebrates. In addition, benthic invertebrate predators were larger in the presence of piscivorous fish, which were negatively correlated with nonpiscivorous fish.

Effects on Periphyton

In two experiments performed in successive years, periphyton biomass doubled in the presence of fish. The results of the enclosure/exclosure experiments, designed to identify the cause of this increase, suggest that fertilization of the channel water by fish is not the cause because periphyton biomass was high in the cages protected from the grazing of large invertebrates, both in the presence and absence of fish. In contrast, the periphyton biomass decrease observed in the cages containing *Baetis* nymphs suggests that this insect may play an important role in the control of algal growth. In this sense, the limitation of the fish effect on channel periphyton on the first sampling date appears to be related to the presence of large *Baetis* nymphs, whose biomass was significantly lower in the presence of fish. The reduction in the biomass and individual size of *Baetis* after the first sampling date was probably associated with its life history. During the latter part of the 1988 and 1989 experiments, emerging adults of *Baetis* were repeatedly collected from channels, and one of the species present (*B. flavistriga*) is known to emerge during July and August in streams in the Canadian Shield (Harper and Harper 1982).

Although *Baetis* is not a typical grazer and is usually classified as a collector–gatherer (Merritt and Cummins 1984), there is evidence that its growth and production can be limited by the availability of algal food (Fuller et al. 1986; Wallace and Gurtz 1986). In addition, Wilzbach (1990) observed a particular feeding strategy in this genus which allows it to graze on periphyton by ripping loose attached algae from the substrate.

The periphyton decrease in cages with *Baetis* was similar in channels with and without fish, which suggests that the total grazing activity of *Baetis* in cages protected from predation was not affected by the presence of brook trout. Kohler and McPeek (1989) observed that in the presence of mottled sculpin (*Cottus bairdi*), the feeding activity of *Baetis* was severely reduced during the day, even though the fish were confined in a channel system designed to avoid physical contact of fish with the nymphs. However, *Baetis* continued to feed at night, which could explain the lack of difference between cages in the presence and absence of fish.

The other two invertebrates used in the cage experiments (*P. subborealis* and *E. aurivillii*) did not reduce periphyton biomass. Analysis of the stomach contents of *P. subborealis* suggests that this trichopteran might affect the periphyton by ingesting loose organic detritus, including decaying algae. However, if such an effect were present, the enclosure/exclosure experiments did not permit its detection.

The control of primary production by cascading trophic interactions or "top-down" effects has been observed in many aquatic systems, including both planktonic and benthic communities (Power 1987, 1990; Carpenter and Kitchell 1988; McQueen et al. 1989; Vanni and Findlay 1990; Weber and Lodge 1990). However, this is the first time that such an effect has been observed for periphyton in streams, involving insects and salmonid fish.

The hypothesis of Fretwell (1977) is closely related to the cascading trophic hypothesis, and some of their predictions are similar. Extending the arguments of Hairston et al. (1960), Fretwell predicted that in food chains with an odd number of trophic levels (e.g. the channels with fish in the present study), plants are released from the pressures of herbivory and eventually become limited by resources such as light or nutrients. In food chains with an even number of trophic levels (e.g. the channels without fish), grazers, released from the pressures of predation, control the plant communities.

Power (1990) also observed an increase in algal biomass in the presence of insectivorous fish in a coniferous forest stream. However, when piscivorous fish were present, the algal biomass decreased. The food chain studied by Power was different from ours and involved four trophic levels: macroscopic algae growing in long tufts (*Cladophora*), herbivorous chironomids, two species of insectivorous fish fry and predatory insects, and two species of carnivorous adult fish. In contrast, in the present study, the food chain that affected primary producers was simpler and representative of Canadian Shield streams. It consisted essentially of three trophic levels: periphyton growing in thin layers, herbivorous Ephemeroptera, and allopatric adult trout. In spite of these differences, both studies concur with the hypothesis put forward by Fretwell (1977), relating even and odd numbers of trophic levels with "bottom-up" and "top-down" control of primary producers.

Contrary to the preceding results, in an experiment conducted in a shaded stream, Hill and Harvey (1990) found that fish did not have an indirect impact on periphytic algae, probably because there were no grazers available to the fish, as was the case in the latter part of our experiment. However, light effects explained a major part of the primary productivity when compared with grazing by snails or the presence of fish. Thus, it may be that the role of fish in controlling primary production is more relevant in sunlit, coniferous forest streams, such as in our study and that of Power (1990); than in deciduous forest streams, where light is a more important limiting factor.

Our results suggest that the size-efficiency hypothesis developed by Brooks and Dodson (1965) for planktonic food webs may also be applicable to stream benthos. In the pelagic zone of lakes, the presence of size-selective planktivorous fish may reduce competitively superior grazers (e.g. *Daphnia*, Cladocera) or invertebrate predators (e.g. *Chaoborus*, Diptera). This permits the development of a zooplankton community composed of small-sized species (e.g. *Bosmina* and *Diaphanosoma*, Cladocera). Similarly, the size-dependent elimination of *Baetis* and *P. subborealis* by trout and the increase in small-sized chironomid densities suggest the existence of analogous mechanisms of interaction in our stream system.

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Size Selectivity of Diamond and Square Mesh Codends in Pelagic Herring Trawls: Only Small Herring Will Notice the Difference

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A twin codend trawl was fished in the northern Baltic to study the size selectivity of square mesh and diamond mesh codends of 36-mm nominal mesh size. For each codend, 15 hauls were completed with a small mesh (20 mm) codend deployed on the other side of the trawl. The relative size of the catches in the two sides of the trawl varied considerably from haul to haul (the separator section was not operating properly) and selection curves were estimated from each individual haul using a method that incorporated the differences in catching efficiency of the two sides. The length of 50% retention decreased with increased catch for both the diamond and square mesh codends, although in neither case was this relationship statistically significant. Selection curves fitted to the combined haul data were asymmetric. The square mesh codend retained significantly less small herring than the diamond mesh codend, and for larger herring the two codends had similar selectivity. In both codends, most escapes occurred at the front of the catch bulge, from the upper side of the codend. At high catch rates, mesh blockage was observed for several metres ahead of the catch bulge during the later part of the tow.

On a utilisé dans le nord de la mer Baltique un chalut à double cul pour étudier la sélectivité par taille de culs de chaluts à mailles carrées et à mailles en losange de 36 mm de maillage nominal. Pour chaque cul de chalut, on a effectué 15 traits avec un cul de chalut à petit maillage (20 mm) déployé de l'autre côté du chalut. La taille relative des captures des deux côtés du chalut variait considérablement d'un trait à l'autre (la nappe séparatrice ne fonctionnant pas correctement), et on a estimé les courbes de sélection pour chaque trait à l'aide d'une méthode qui intégrait les différences dans l'efficacité de capture des deux côtés. La longueur de courbe à 50 % de rétention diminuait avec l'augmentation des prises pour les deux types de maille, mais dans aucun cas la relation ne se révélait significative statistiquement. Les courbes de sélection ajustées aux données des traits combinés étaient asymétriques. Le cul à mailles carrées retenait nettement moins de petits harengs que le cul à mailles en losange, et pour les harengs de plus grande taille, les deux culs avaient une sélectivité similaire. Dans les deux cas, les échappées se produisaient pour la plupart à l'avant du renflement de la prise, par la phase supérieure du cul de chalut. Lorsque le taux de capture était élevé, on observait un blocage des mailles sur plusieurs mètres en avant du renflement des captures pendant la dernière partie du trait.

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Trawlers fishing for Atlantic herring (*Clupea harengus*) in the northern Baltic Sea frequently catch a high proportion of small herring when using the legal minimum codend mesh opening of 16 mm (measured when wet). Small herring are often discarded because of the weak and unstable markets for low-value fodder fish. Studies into the selectivity of larger and different shaped meshes have been prompted by the desire to reduce this catch of small fish, thereby reducing both wastage and the physical effort of sorting.

The size selectivity of 32-mm (whole mesh length) diamond and 33-mm hexagonal mesh codends in pelagic herring trawls was assessed in the Gulf of Finand (ICES subdivision 32) by Suuronen et al. (1991). The experiments were conducted in October 1989 and October 1990 on a 300-hp Baltica class stern trawler using the covered codend (1989 only) and trouser trawl methods (both years). There was strong indication that the cover had influenced herring escape behaviour and the covered codend data were considered invalid (Järvik and Suuronen 1990). For the 32-mm diamond mesh codend, Suuronen et al. (1991) estimated 50% retention lengths (l_{50}) of 13.8 and 13.5 cm and selection ranges (l_{75}–l_{25}) of 4.2 and 3.8 cm from the 1989 and 1990 trouser trawl data, respectively. The 33-mm hexagonal mesh codend (data from 1990 only) had a substantially lower l_{50} of 12.5 cm. Both these codends retained a large number of small herring, and a more selective codend is desirable provided that the loss of larger fish is slight.

Comparisons of the size selectivity of round groundfish by square and diamond mesh codends in bottom trawls have generally shown that, for a given mesh, a square mesh codend has higher l_{50} and narrower selection range than diamond (e.g. Robertson and Stewart 1988; Cooper and Hickey 1989). Shevtsov (1988) reported on Soviet studies made in the eastern Baltic, where a square mesh codend in a herring bottom trawl was found to release more small herring than a diamond mesh codend of the same mesh. However, the selectivity of pelagic trawls may be different, since they are generally much larger gears with disproportionately longer codend extension pieces and have higher catch rates than bottom trawls.

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The results of selectivity experiments conducted with 36-mm diamond and square mesh codends in pelagic herring trawls are presented here. The experiments deployed an underwater video camera to monitor the codends and to observe the behaviour of herring in the codends. The statistical analysis of the catch data uses the SELECT (**S**hare **E**ach **LE**ngthclass's **C**atch **T**otal) method of Millar (1992), as applied to trouser trawls by Millar and Walsh (1992). In addition to analysis of the data combined over hauls, selection curves are also fitted to individual haul data so that the effects of catch size and haul duration can be examined. The selectivity results obtained are discussed with regard to the observed behaviour of herring and the performance of the experimental gear.

Materials and Methods

Fishing Trials

Selectivity experiments were carried out from 7 May to 7 June 1990 in the Archipelago Sea (ICES subdivision 29N) on the fishing ground off northeastern Nauvo. A standard 96 × 3200 mm herring midwater trawl (Fig. 1) was modified into a trouser trawl by inserting a separator section behind the belly. The separator section was connected to the trawl at the point where its circumference was equal to that of the trawl. A vertical netting panel inside the separator section divided it into two "equal" legs (Fig. 2) to which two codends of commercial size were attached by means of plastic rings joined together by rope. The codends were switched at convenient intervals during the course of the experiment.

The two experimental codends were made of the same knotted PA netting (36-mm nominal whole mesh length), had the same number of meshes in their circumference, and were of the same stretched length (Fig. 2). The small mesh (20-mm whole mesh length) codend is a standard codend used by trawlers. In order to stretch the meshes into their effective working shape, both large mesh codends were used in the commercial fishery for a period of about 1 mo prior to the selectivity trials.

Throughout the selectivity trials the inside mesh opening of the codends was measured with a flat wedge-shaped gauge, pushed gently by hand into the meshes. The mesh opening varied from 29 to 32 mm in the extension piece of the large-mesh codends, from 32 to 35 mm in the few mesh rows in front of the lifting bag, and from 29 to 32 mm in the lifting bag. The square mesh codend had on average a 1- to 1.5-mm larger mesh opening than the diamond mesh codend, the difference being most marked in the extension. It was also noted that the shape of the square meshes had changed slightly, having elongated to a somewhat rectangular shape, especially in front of the lifting bag. The average mesh opening of the small mesh codend was approximately 15 mm.

Experimental fishing was carried out during the daytime under normal commercial fishing conditions aboard the chartered side trawler *Mia* (32.5 m, 850 hp). Two typical echograms of the fishing ground are shown in Fig. 3. The headline height of the trawl was about 20 m. The trawl was towed at the depth of maximum fish concentration; tow duration averaged about 1.5 h and towing speed, measured by a propeller log, varied from 3.0 to 3.3 kn. Successive tows were generally performed in opposite directions on the fishing ground. The water temperature at fishing depth was 7–9°C. An underwater video camera was mounted on a simple self-made foil that was towed by a small boat attached by rope to the headline of the trawl and was primarily used to monitor the large mesh codends.

A sample of 8–22 kg was taken from each codend on each successful tow and each herring in the sample was measured to the nearest 0.5 cm. The ratio of codend catch weight to sample weight was used to scale up the length class frequencies of herring in the sample to give estimated length class frequencies for the entire codend catch of herring.

SELECT Analysis

We chose to use the SELECT method of analysis (Millar 1992). It is based on a general statistical model that applies to most selectivity studies, including hook and gillnet studies where many different sizes and/or shapes of the fishing gear are used. The application of SELECT to trouser trawls configured with a nonselective small mesh (control) codend and an experimental codend is given in Millar and Walsh (1992) and is briefly explained below.

The SELECT method incorporates the possibility of unequal fishing efficiencies of the two codends by defining a "split" parameter p to be the probability that a fish entering the trouser trawl will enter the experimental codend. It is assumed that p is independent of the fish's length. The selection curve of the experimental codend will be denoted by $r(l)$, the probability that a length l fish will be retained given that it entered that codend. If a fish of length l enters the trouser trawl, then the probability that it is caught in the experimental codend is the product of the probability that it enters the experimental codend and the probability that it is then retained, that is, $p \times r(l)$. The probability that it is caught in the small mesh codend is simply the probability that it enters that codend, $1 - p$. Simple conditional probability enables one to conclude that the probability that a fish of length l is caught in the experimental codend, given that it is caught in the trouser trawl, is

$$(1) \quad \frac{p \times r(l)}{(1-p) + p \times r(l)}.$$

The rationale behind the SELECT method is, for every length class, to fit the above probability to the observed proportion of the length class's total (experimental plus small mesh codend) catch that was caught in the experimental codend. Parameter p and the parameters of the selection curve are estimated by maximum likelihood as described in Millar and Walsh (1992). The maximum likelihood model assumes that the observed proportion of each length class's total catch that is taken by the experimental codend arises from a binomial distribution (Millar 1992). Millar and Walsh (1992) included formulae for the standard errors of the estimated parameters and estimated selection lengths, such as l_{50}.

An alternative selectivity analysis would be to use the "traditional" approach described in Pope et al. (1975). Assuming that the two codends have equal fishing efficiency, the traditional analysis fits a selection curve to the ratios of experimental over small mesh codend catches (by length class). This implicitly assumes that the number of fish in each length class that entered the (nonselective) small mesh codend gives the number that entered the experimental codend, and consequently the catch ratios are often called the "proportions retained." Clearly, they are not proportions, but nonetheless the traditional fits to these ratios use statistical techniques for analysing proportions (e.g. logit or probit analysis). Note that this requires data manipulation because whenever a catch ratio exceeds 1.0,

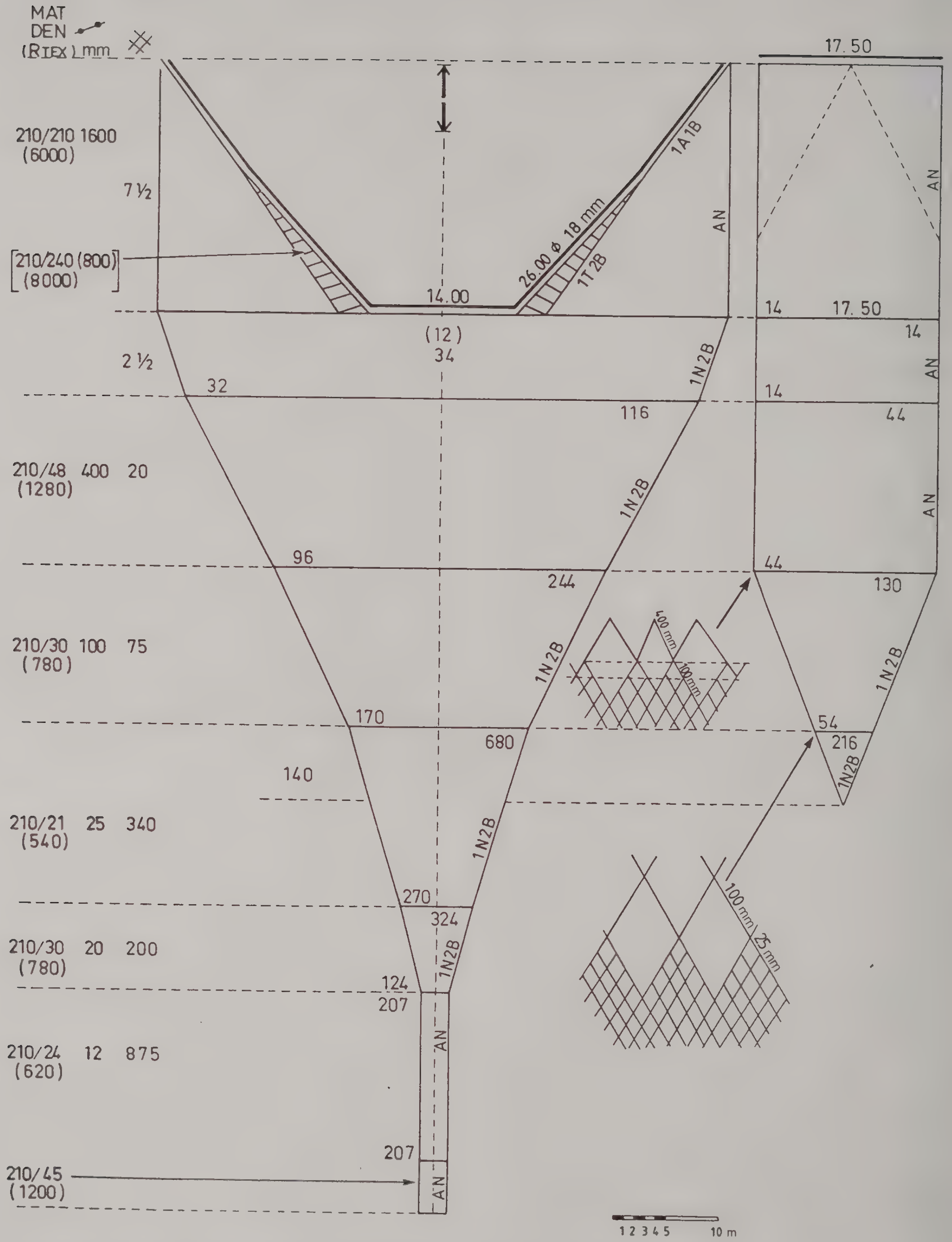
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FIG. 1. Schematic showing the top panel (bottom panel identical) and side panel of the "standard" pelagic trawl prior to modification into a trouser trawl. (Note: In this schematic only, the mesh sizes are expressed as half mesh size.)

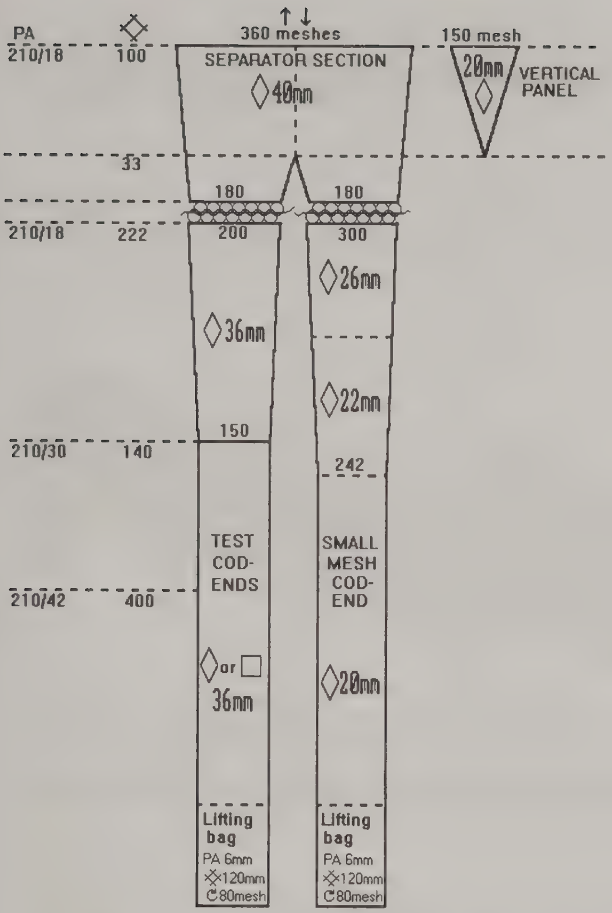


FIG. 2. Schematic of the separator section and the experimental and control (small mesh) codends used to modify the standard pelagic trawl into a trouser trawl.

that length class must be discarded or the ratio set to 1.0. Being without a sound statistical framework the properties of the traditional analysis are largely unknown. Cadigan and Millar (1992) have used simulation to show that it can suffer from severe biases and does not perform as well as SELECT. The traditional analyses require further ad hoc data manipulation if the two codends fish with unequal efficiency. The absence of such data manipulation in SELECT is the reason that Fonteyne (1991) recommended SELECT over the traditional analysis.

Results

A total of 36 tows were completed, but the data from two tows were rejected because of severe gear problems. Of the remaining 34 tows, 30 were performed using the small mesh control codend on one side and an experimental codend on the other side. Fifteen hauls with each experimental codend were completed in this way. The other four hauls fished the two experimental codends simultaneously. The sequence of codends used in the tows is presented in Table 1.

The catches consisted almost solely of herring. An average of 462 herring were taken from each codend on each successful haul (31 447 total). Tables 2 and 3 give the estimated length class frequencies combined over the hauls performed with the large mesh/small mesh codend combination. The almost identical length distribution of the two small mesh codend data sets (Fig. 4a) implies that the two experimental codends were sampling fish of the same size composition. The three distinct modes at 9, 15 and 17 cm are largely due to age 1, age 2, and older fish, respectively. Figure 4b shows that above a length of 16 cm the two large mesh codends caught similar numbers of fish. Below 16 cm the experimental diamond mesh codend catch was almost 2.5 times greater than the square mesh codend catch. In the small mesh codend, 28.2% of the herring were below 12 cm (mostly age 1 fish) whereas in the experimental codends, these percentages were 4.2 and 0.2 for diamond and square mesh, respectively.

The average catch per tow (1700 kg) was similar to that of the commercial fishery, but being split between two codends the average catch in each codend was therefore smaller than the commercial average. The catches showed large between-haul variation, and unexpectedly large within-haul variation due to the catch often being considerably higher in one leg of the trawl (Table 1). In five of the first eight hauls, the catch was larger on the port side of the trawl. The separator section was then turned around. Thereafter the starboard side appeared to be favoured and had equal or better catch in 22 of the 26 subsequent successful hauls. These 26 hauls include the four hauls in which the two experimental codends were fished simultaneously, and in all four cases the catch was larger on the starboard side. An attempt was made after haul 27 to improve the construction of the codend attachment system, but only with minor effect on the unequal catching performance of the codends.

These findings strongly suggested that the separator section did not give equal catching performance to the two legs of the trawl. The underwater video frequently showed the number of fish entering the separator section to be much greater in one of the two legs, and on occasion the legs of the separator section were seen to be of different shape with corresponding distortion of the vertical separator panel. In addition, on every turn of the trawler, fish were herded more along the outer wall of the separator section and into the outer codend.

Escape Behaviour

The visibility obtained by the underwater video camera was limited to at best 3 or 4 m due to the turbid water of the Baltic Sea. Nonetheless, some interesting features on the behaviour of herring in a pelagic trawl codend were observed. The herring generally swam inside the trawl belly and the codend extension in the towing direction, mostly keeping close to the upper panels. Gradually the fish dropped back towards the after part of the codend, where most still swam actively for a short period. Fish were occasionally observed escaping through the gaps at the joins of the separator section and codends. When the trawl caught a larger number of fish in a short time, some escape through the meshes of the separator section was also observed.

During towing, the small mesh codend extension piece maintained a generally round shape. The extension pieces of both large mesh codends were mostly slack and distorted and the meshes of the square mesh extension were generally more open than the meshes of the diamond mesh extension. However, in both experimental codends, most escapes were seen to occur at the front of the catch bulge, in the upper side of the after part of the codend. The after part of all codends were bulbous, even with very small catches, and the meshes were predominantly open. No clear difference in the escape process of fish

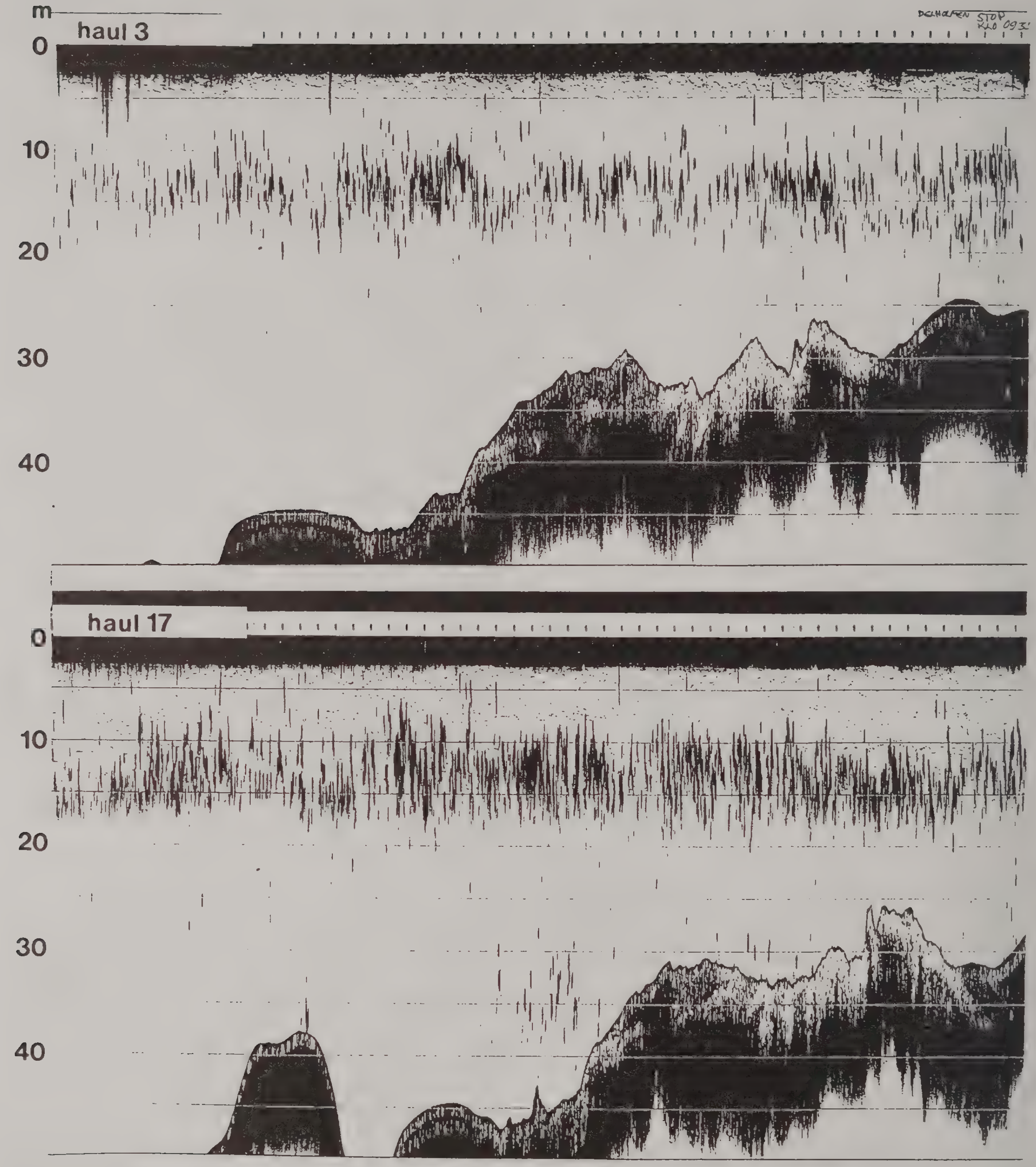


FIG. 3. Typical echograms of the fishing ground off Nauvo during the fishing trials in May–June 1990. The small herring schools are mostly at a depth of 10–15 m.

through the experimental square and diamond mesh codends was observed.

Mesh blockage was observed in some of the higher catch hauls. It appeared that weakened herring were pushed against the meshes by the water flow and at times the codend walls were lined with herring for several metres in front of the catch bulge. During some of the higher catch hauls the codends were seen to undulate, causing turbulence inside the codend. Fish were waved backwards and forwards, and from side to side, often striking the meshes and each other. The process of active escape appeared to be hindered under these circumstances.

Herring swimming inside the large mesh codends generally made more attempts to escape than herring swimming inside the small mesh codend. The passage of herring through the

TABLE 1. Sequence of codends used in the port and starboard legs of the trouser trawl, and their catches.

Haul No.	Date	Codend		Catch (kg)	
		Port	Starboard	Port	Starboard
1	7 May	Diamond 36 mm	Small mesh	1 520	850
2	7 May	Square 36 mm	Small mesh	790	355
3	8 May	Square 36 mm	Small mesh	1 150	690
4	8 May	Diamond 36 mm	Small mesh	800	690
5	9 May	Diamond 36 mm	Small mesh	650	940
6	9 May	Small mesh	Square 36 mm	285	145
7	9 May	Small mesh	Square 36 mm	1 420	1 900
8	14 May	Small mesh	Square 36 mm	205	370
		Separator section was turned around			
9	15 May	Diamond 36 mm	Small mesh	580	1 110
10	15 May	Diamond 36 mm	Small mesh	210	550
11	15 May	Square 36 mm	Small mesh	520	1 150
12	16 May	Small mesh	Diamond 36 mm	1 610	1 200
13	16 May	Small mesh	Square 36 mm	195	495
14	21 May	Diamond 36 mm	Small mesh	85	360
15	21 May	Square 36 mm	Small mesh	410	1 020
16	22 May	Small mesh	Diamond 36 mm	930	1 560
17	22 May	Square 36 mm	Small mesh	570	1 450
18	23 May	Small mesh	Diamond 36 mm	840	1 110
19	23 May	Small mesh	Square 36 mm	1 200	1 040
20	24 May	Diamond 36 mm	Small mesh	490	740
21	Rejected				
22	28 May	Square 36 mm	Small mesh	180	590
23	28 May	Diamond 36 mm	Small mesh	260	430
24	28 May	Square 36 mm	Small mesh	475	1 570
25	29 May	Square 36 mm	Diamond 36 mm	890	1 700
26	30 May	Diamond 36 mm	Square 36 mm	1 330	1 700
27	Rejected				
		Adjustment on the rigging of the separator section			
28	4 June	Diamond 36 mm	Small mesh	1 610	1 570
29	4 June	Small mesh	Square 36 mm	1 200	2 000
30	5 June	Diamond 36 mm	Square 36 mm	1 100	1 500
31	5 June	Square 36 mm	Diamond 36 mm	1 000	1 500
32	6 June	Small mesh	Diamond 36 mm	470	470
33	6 June	Diamond 36 mm	Small mesh	90	90
34	6 June	Diamond 36 mm	Small mesh	410	910
35	7 June	Square 36 mm	Small mesh	260	610
36	7 June	Small mesh	Square 36 mm	900	650
In total (kg)				24 635	33 015

meshes occurred at high speed, and with a video camera it was difficult to see any details of the process. No obvious loss of scales was observed and scales seen in the water were mainly from meshed fish and those that were crushed against the netting at the rear of the catch accumulation. Large numbers of herring were observed to continue swimming and to disappear from the view of the camera after passage through the meshes.

Less herring were meshed in the square mesh codend than in the diamond mesh codend, and more herring were seen to escape from the square mesh codend while it was being hauled. Although these herring escaped, they may have been severely damaged.

Selectivity Analysis

The SELECT method was discussed above in the context of the experimental/control codend combination. It can also estimate selection curves from trouser trawl data where two experimental codends are fished simultaneously (i.e. the overlapping selection curves case), but unpublished work by the second author has shown that the estimated selection curve parameters have extremely high variability, unless the two codends have very different selectivity. For this reason, the data from the four tows that fished the 36-mm diamond mesh and 36-mm square mesh codends simultaneously are not used in this present selectivity analysis. Analysis is restricted to the 30 hauls with experimental/control codend combinations.

The underwater video observations suggested that the unequal fishing efficiencies of the codends was caused by inadequacy of the separator section, since it was seen to often fail to split the after part of the trawl into two equal parts. If water flow velocity was different (due to the different size meshes used) in the two sides of the trawl in front of the separator section, then it is possible that a larger proportion of smaller (weaker) fish were herded into the side where the flow was greater, resulting in size-dependent inequality in the fishing efficiency. However, on the basis of observed fish behaviour patterns, no such difference in flow velocity was apparent. Thus we feel that it is reasonable to make the assumption that the split of fish into the two codends is the same for all lengths.

Prior to performing the SELECT analyses, it was noted that the diamond mesh codend catches (Table 2) show an increase in the experimental over small mesh codend catch ratios as

TABLE 2. Combined (over 15 hauls) length class frequencies for the catches of the experimental 36-mm diamond mesh codend and associated small mesh codend, and the experimental over small mesh codend catch ratios.

Length (cm)	No. of fish in 36-mm codend (diamond)	No. of fish in small mesh codend	Catch ratio (× 100)
6.5	0	0	
7.0	0	200	0.0
7.5	155	1 630	9.5
8.0	421	7 775	5.4
8.5	1 058	18 806	5.6
9.0	2 646	30 899	8.6
9.5	3 093	26 386	11.7
10.0	2 361	19 106	12.4
10.5	1 326	10 224	13.0
11.0	377	5 423	7.0
11.5	436	5 100	8.5
12.0	492	5 043	9.8
12.5	617	2 786	22.1
13.0	431	2 838	15.2
13.5	787	3 805	20.7
14.0	4 225	13 974	30.2
14.5	8 152	19 678	41.4
15.0	12 661	29 669	42.7
15.5	9 086	16 134	56.3
16.0	12 716	17 897	71.1
16.5	16 376	19 645	83.4
17.0	24 381	28 247	86.3
17.5	20 438	25 879	79.0
18.0	22 550	24 316	92.7
18.5	19 888	17 316	114.9
19.0	20 923	16 955	123.4
19.5	17 617	16 603	106.1
20.0	17 005	15 288	111.2
20.5	11 754	9 760	120.4
21.0	13 423	12 834	104.6
21.5	9 737	8 674	112.3
22.0	8 804	6 402	137.5
22.5	4 987	5 439	91.7
23.0	4 802	4 627	103.8
23.5	3 397	2 723	124.8
24.0	2 386	2 140	111.5
24.5	1 599	1 291	123.9
25.0	916	838	109.3
25.5	829	551	150.4
26.0	456	628	72.6
26.5	153	271	56.6
27.0	754	188	402.1
27.5	144	39	371.3
28.0	0	117	0.0
28.5	134	59	227.5
29.0	0	49	0.0
In total	284 493	458 251	

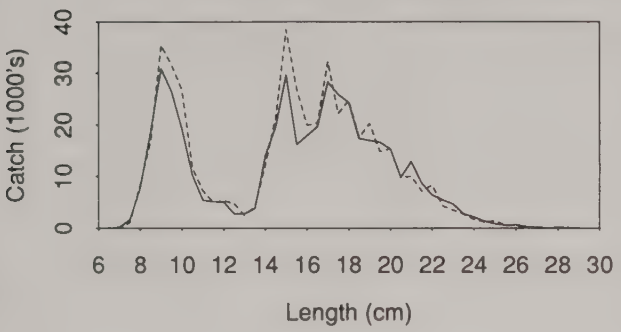
TABLE 3. Combined (over 15 hauls) length class frequencies for the catches of the experimental 36-mm square mesh codend and associated small mesh codend, and the experimental over small mesh codend catch ratios.

Length (cm)	No. of fish in 36-mm codend (square)	No. of fish in small mesh codend	Catch ratio (× 100)
6.5	0	102	0.0
7.0	0	47	0.0
7.5	0	1 125	0.0
8.0	66	8 485	0.8
8.5	17	16 896	0.1
9.0	78	35 447	0.2
9.5	62	31 589	0.2
10.0	48	26 708	0.2
10.5	77	11 669	0.7
11.0	32	7 229	0.4
11.5	0	5 029	0.0
12.0	88	5 313	1.7
12.5	125	4 754	2.6
13.0	184	2 436	7.6
13.5	344	4 209	8.2
14.0	1 691	12 252	13.8
14.5	3 684	21 488	17.1
15.0	8 382	38 411	21.8
15.5	5 112	26 931	19.0
16.0	11 632	19 933	58.4
16.5	16 907	20 331	83.2
17.0	27 626	32 287	85.6
17.5	23 268	22 164	105.0
18.0	23 779	24 746	96.1
18.5	18 648	17 551	106.3
19.0	22 265	20 232	110.0
19.5	17 792	14 815	120.1
20.0	18 667	15 347	121.6
20.5	12 612	9 825	128.4
21.0	11 091	9 978	111.2
21.5	9 593	7 138	134.4
22.0	6 932	8 307	83.4
22.5	5 813	4 262	136.4
23.0	4 017	3 481	115.4
23.5	2 422	2 703	89.6
24.0	2 681	1 646	162.9
24.5	2 109	1 172	179.9
25.0	1 166	1 390	83.9
25.5	286	540	52.9
26.0	853	485	175.8
26.5	399	319	125.2
27.0	23	181	12.6
27.5	282	80	253.6
28.0	23	112	20.4
28.5	197	92	213.7
29.0	148	0	
In total	261 155	499 235	

length increases from 8.0 to 10.5 cm, but then an unexpected decrease for lengths from 11.0 to 12.0 cm. It was felt that this could be caused by escapement of the very small fish (10.5 cm or less, say) from the small mesh codend. That would cause the small mesh codend catches of these fish to be underestimated, resulting in overestimation of the catch ratio. The underwater camera spent little time monitoring the small mesh codend and so a limited amount of escapement could have gone unnoticed. Rather than have the SELECT method estimate the small mesh codend's selection curve (a considerably more difficult analysis), we decided to adjust its catches under the assumption that it had a logistic selection curve with a 50% retention length of 8.5 cm and selection range of 2 cm. It is noted in the Discussion section that the analyses were not much affected by this adjustment.

Figures 5 and 6 show the SELECT fits to the 30 individual hauls. These fits used a logistic $r(l)$ in equation (1). The height of the fitted curve is the estimate of p, the proportion of fish entering the large mesh codend (Millar and Walsh 1992). It is clear that this varies greatly between hauls. Table 4 gives the estimated 50% retention lengths, their standard errors and 95% confidence intervals, and the estimated selection ranges. The sample sizes used in these analyses are those of the measured samples, scaled to represent the same fraction of total catch. For example, if the measured samples from the large and small mesh codends correspond to 3 and 2% of their catch, respec-

a. Small mesh codend catches



b. Experimental codend catches

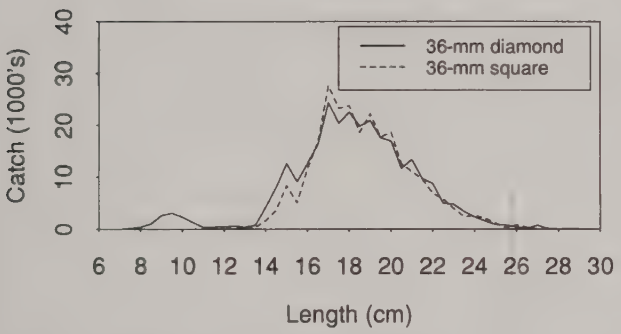


FIG. 4. Combined length frequencies distributions of the (a) small mesh codend catches and (b) experimental codend catches. The solid and broken lines in Fig. 4a represent the small mesh codend hauls associated with the experimental diamond and experimental square mesh codends, respectively.

tively, then the length class frequencies in the large mesh sample are reduced by one third so that they also correspond to 2% of that codend's catch. Although this results in some noninteger frequencies, it does not affect the analysis. The very same selection curve would be fitted using the estimated total codend catch length class frequencies, but the estimates of standard error and goodness of fit would be inappropriate.

The diamond fits are quite consistent with the exception of hauls 10, 28, and 33. In the latter two hauls the split of fish into the large mesh codend is estimated to be much greater than 50%. From Fig. 5, one sees that the data from these hauls do not give much indication of what the height of the fitted curves should be. This uncertainty is reflected in the wide confidence intervals for l_{50}, which both encompass ''reasonable'' values for l_{50}. The results for the square mesh codend are very consistent; in fact, 10 of the 15 estimated l_{50}'s fall within a 1-cm interval (15.8–16.8 cm). The selection ranges are noticeably smaller for the square mesh codend.

Figure 7 shows plots of the estimated l_{50}'s versus the weight of catch in the large mesh codend and the fitted (weighted) linear regression line. (Each point was weighted by the inverse of the variance of the estimated l_{50}.) The vertical axis on both plots is over the range 14–18 cm and so the l_{50}'s from the three 36-mm diamond mesh hauls mentioned above are absent from the plot, although they were used in the fit of the linear regression line. For both codends the regression line has negative slope. The diamond mesh regression line gives a reduction in l_{50} of 0.16 cm per 1000 kg of catch. For the square mesh, this reduction is 0.14 cm per 1000 kg. The standard errors of these values are 0.46 and 0.30, respectively, so neither slope is significantly different from zero. Haul duration was also used as an explanatory variable, but did not lead to any statistically significant effects either by itself or fitted with catch size. (In fact, increased haul duration corresponded to increased l_{50} for the diamond mesh codend and decreased l_{50} for the square mesh codend.)

The fits to the individual hauls are reasonably consistent, and there is no significant effect of catch size or haul duration, so analyses on the catches combined over hauls were performed. The numbers of very small herring that were retained by the experimental diamond mesh codend suggest that the selection curve may not be symmetric, but instead have a longer ''tail'' on the left corresponding to relatively high probability of retention of small fish. So, in addition to fitting (symmetric) logistic selection curves the asymmetric selection curve used by Millar (1991) was also fitted. Denoting retention probability by $r(l)$, this curve is given by

$$(2) \quad r(l) = \left(\frac{\exp(a + bl)}{1 + \exp(a + bl)} \right)^{1/\delta}$$

where a, b, and δ are parameters to be estimated. This curve is commonly known as the Richards curve in the context of growth studies. It is a generalization of the logistic selection curve and allows one to test the hypothesis that the selection curve is logistic ($\delta = 1$) versus the alternative that it is asymmetric. Values of δ less than 1 correspond to a longer tail on the right and δ greater than 1 to a longer tail on the left. Note that it was not attempted to fit the asymmetric curve to the individual haul data because Millar (1991) used simulation to show that a sample size of several thousand is required for reliable fits of this curve to trouser trawl data.

The maximum likelihood fit of logistic selection curves resulted in l_{50}'s of 16.0 and 16.4 cm and selection ranges of 4.7 and 2.1 cm for the diamond and square mesh codends, respectively (Table 5). The deviance values in Table 5 are the likelihood ratio test statistics for the hypotheses in question. In particular, hypothesis H_1 (testing goodness of fit) rejected the fit of the logistic selection curves at the 5% level, with p-values of 0.02 and 0.0003 for the diamond and square mesh codends, respectively.

The hypotheses of symmetry H_2: $\delta = 1$ were rejected by the likelihood ratio test (Table 5) with p-values of 0.001 for both experimental codends. These tests indicate that the asymmetric curves (equation 2) provided significant improvements in fit over the logistic. For the asymmetric selection curves, the fit to the diamond mesh codend data was adequate (p-value = 0.10) but the square mesh codend fit was not (p-value = 0.003). (For now, we ignore this lack of fit and address its consequences in the Discussion section.) The maximum likelihood fits to the observed proportions of catch in the experimental codend of the probabilities defined in equation (1), using the asymmetric $r(l)$'s, are given in Fig. 8. The deviance residuals plotted in this figure are the signed square roots of the length class's contribution to the likelihood ratio statistic for testing model fit (McCullagh and Nelder 1989, p. 39).

A likelihood ratio test rejected the hypothesis that the two large mesh codends had the same (asymmetric) selection curves (p-value $< 10^{-6}$). The asymmetric curves gave l_{50}'s of 15.6 and 16.2 cm and selection ranges of 3.5 and 1.6 cm for the diamond and square mesh codends, respectively (Table 5).

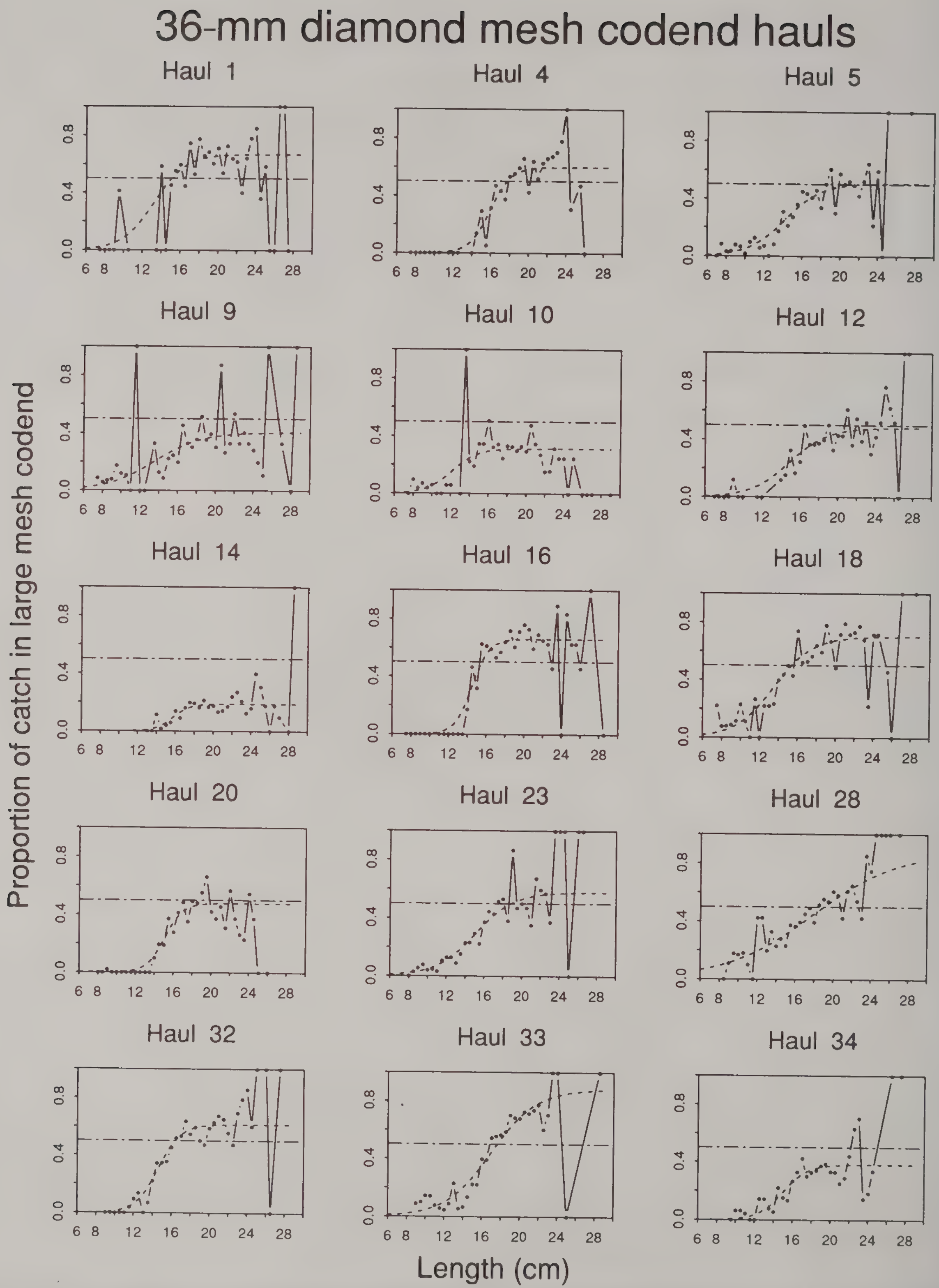


FIG. 5. Plots of the proportion of each length class's total catch taken by the 36-mm diamond mesh codend for each of the 15 individual hauls. The curves fitted to these data by maximum likelihood are overlaid.

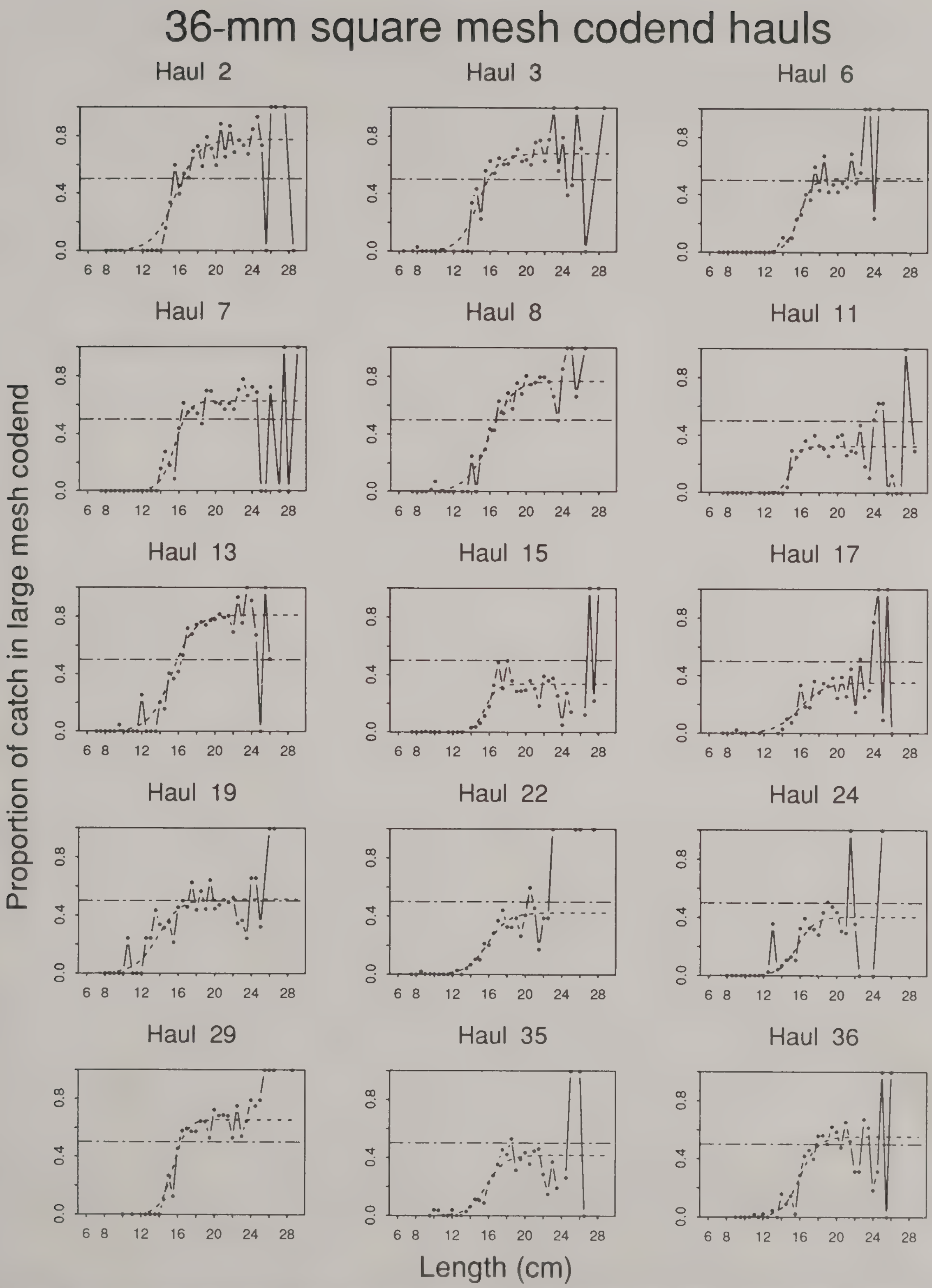


FIG. 6. Plots of the proportion of each length class's total catch taken by the 36-mm square mesh codend for each of the 15 individual hauls. The curves fitted to these data by maximum likelihood are overlaid.

TABLE 4. Estimated 50% retention lengths (l_{50}), their standard errors and 95% confidence intervals, and the estimated selection ranges (l_{75}–l_{25}) for the individual hauls.

Haul	l_{50}	SE	95% CI for l_{50}	Selection range
36-mm diamond mesh codend hauls				
1	15.1	1.1	12.8–17.4	3.7
4	16.9	0.5	16.0–17.9	2.4
5	15.6	1.0	13.6–17.6	4.2
9	14.8	1.8	11.2–18.5	5.5
10	12.7	1.3	10.0–15.3	3.0
12	16.2	1.1	13.9–18.6	4.4
14	15.9	0.8	14.3–17.5	2.0
16	15.5	0.4	14.6–16.3	2.0
18	15.9	0.9	14.1–17.8	4.4
20	15.7	0.4	14.9–16.6	2.1
23	16.8	1.4	14.1–19.6	4.5
28	27.7	13.4	0.8–54.6	10.1
32	15.7	0.4	14.9–16.6	2.6
33	22.2	3.1	16.0–28.4	5.3
34	15.6	0.7	14.2–17.1	2.9
36-mm square mesh codend hauls				
2	17.4	0.8	15.9–18.9	2.7
3	15.9	0.5	15.0–16.9	2.4
6	16.3	0.5	15.4–17.2	1.6
7	16.3	0.4	15.5–17.0	1.7
8	17.9	0.5	16.8–18.9	2.8
11	15.1	0.5	14.0–16.2	1.1
13	17.3	0.6	16.2–18.5	2.7
15	15.8	0.5	14.8–16.8	1.4
17	16.5	0.7	15.0–17.9	2.9
19	14.7	0.5	13.7–15.6	2.7
22	16.5	0.8	14.8–18.1	2.5
24	16.1	0.6	15.0–17.3	2.0
29	16.3	0.3	15.7–16.9	1.6
35	16.3	0.5	15.3–17.4	2.2
36	16.8	0.5	15.9–17.7	2.1

These l_{50}'s correspond to selection factors (the ratio of l_{50} to mesh size) of 4.3 and 4.5, respectively. The estimated asymmetry parameters δ were estimated to be 2.9 and 2.7, respectively, both corresponding to the selection curve having a longer tail on the left. The estimated asymmetric selection curves are shown in Fig. 9.

The fits of the selection curves also included estimation of the split parameter p, the proportion of fish that entered the larger mesh codend. For both the diamond and square mesh codends, p was estimated to be 0.53 (from the asymmetric curve fits) and the hypotheses of equal split H_3:$p = 0.5$ were rejected with p-values less than 0.001.

Discussion

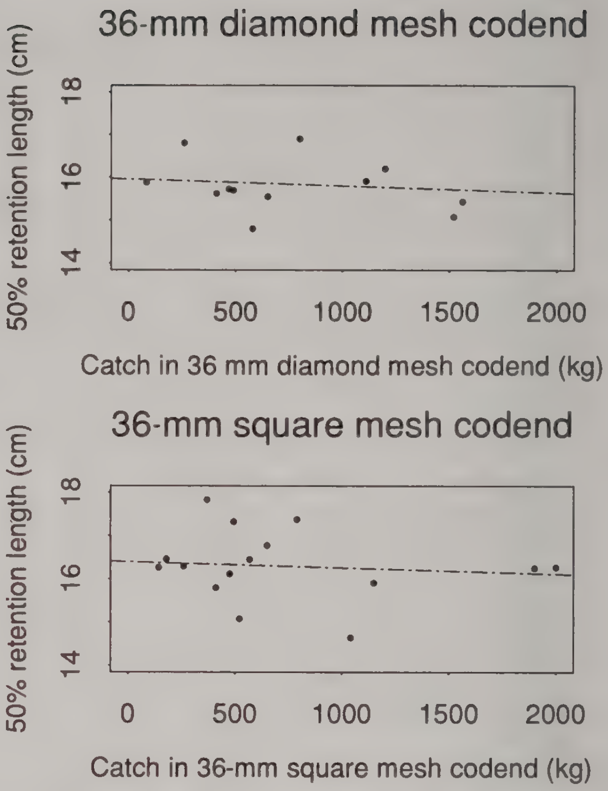


FIG. 7. Weighted least squares linear regression of the l_{50}'s estimated from the individual hauls against catch size.

The standard errors given in Table 5 were calculated from the expected Fisher information matrix (Lehmann 1983) for a, b, δ, and p and as such require large sample sizes to be accurate. Millar (1991) has shown that the sample sizes (number of herring measured) of 13 304 and 13 271 for the combined data from the diamond/small mesh codend combination hauls and square/small mesh codend combination hauls, respectively, are sufficiently large. The standard errors enable one to conclude that the l_{25} of the diamond mesh codend is signficantly lower than that of the square mesh codend. The same is true of the l_{50}'s, but the l_{75}'s are not significantly different. These inferences are very consistent with the combined length distribution plots (Fig. 4a and 4b) which suggest that the greatest difference between the codends is for smaller fish.

The above inferences are subject to a bit of "fuzziness." For example, the correction for selectivity of the small mesh was somewhat arbitrary, as it was difficult to detect escapement of these very small fish using the underwater camera. To check the effect of this correction the asymmetric selection curves were also fitted to the uncorrected data. There was no change to the square mesh codend fits. For the diamond mesh codend, this gave estimated l_{25}, l_{50}, and l_{75} of 13.3, 15.7, and 17.2 cm, respectively. These values are very close to the values 13.6, 15.6, and 17.1 cm from Table 5. Certainly, the inferences of the previous paragraph do not change.

Another source of criticism is that the asymmetric fit to the square mesh codend showed significant lack of fit (p-value = 0.003). Figure 8 shows a very large residual at 15.5 cm, but no systematic lack of fit of the asymmetric Richard's curve is suggested. The lack of fit is therefore due to overdispersion (extra binomial variation) and/or between haul variation. Overdispersion may arise because the schooling of herring violates the assumption, implicit in the binomial maximum likelihood model used by SELECT, that fish entering the codends behave in a (statistically) independent manner. However, since the codend catches were subsampled, the effect of this behaviour will largely be mitigated. Overdispersion is common in the statistical analysis of binary data and is known to have little effect on the estimated parameters (McCullagh and Nelder 1989, p. 126), but it does increase their standard errors and affect the likelihood ratio tests. The standard errors are corrected through

TABLE 5. Selection curve parameters and hypothesis tests. The logistic curve corresponds to $\delta = 1$. Standard errors are given in parentheses. Hypothesis H_1 tests goodness of fit of the curves. Hypothesis H_2 tests $\delta = 1$, the hypothesis that the selection curve is logistic. Hypothesis H_3 tests $p = 0.5$, the hypothesis of equal fishing efficiency of the small (20-mm) and large (36-mm) mesh codends.

	36-mm (whole mesh length) diamond mesh codend		36-mm (whole mesh length) square mesh codend	
	Logistic curve	Asymmetric curve	Logsitic curve	Asymmetric curve
a	−7.4	−18.8	−16.9	−38.5
b	0.46	1.1	1.0	2.3
δ		2.9		2.7
p	0.57	0.53	0.55	0.53
l_{25}	13.7	13.6 (0.1)	15.3	15.3 (0.1)
l_{50}	16.0	15.6 (0.2)	16.4	16.2 (0.1)
l_{75}	18.4	17.1 (0.3)	17.4	16.9 (0.1)
Selection factor	4.5	4.3	4.5	4.5
Selection range	4.7	3.5 (0.3)	2.1	1.6 (0.1)
H_1: Model fit				
Deviance	68.2	57.6	87.7	76.7
df	46	45	47	46
p-value	0.02	0.10	0.0003	0.003
H_2: Logistic curve, $\delta = 1$				
Deviance		10.6		11.0
df		1		1
p-value		0.001		0.001
H_3: Equal fishing efficiency, $p = 0.5$				
Deviance		14.3		17.5
df		1		1
p-value		<0.001		<0.001

multiplying by $\hat{\sigma}$ where $\hat{\sigma}^2$ (the scale factor) is the ratio of model deviance to degrees of freedom (df) from hypothesis H_1 (goodness of fit). The deviance values of the hypothesis tests for symmetry and equal split ($p = 0.5$) are divided by $\hat{\sigma}^2$. For the diamond mesh codend, $\hat{\sigma}^2 = 57.6/45 \doteq 1.28$ and $\hat{\sigma} = 1.13$. For the square mesh codend, $\hat{\sigma} = 1.29$. These corrections do not change any of the inferences made earlier.

Fryer (1991) showed that the above correction using the model deviance is not capable of compensating for between-haul variation. Had the individual haul fits shown a significant relationship with catch size or haul duration, it may have been possible to model structural components of this variation. Without structural relationships, we again can only incorporate this extra variation by adjusting the deviance values and the standard errors of the estimated parameters. Instead of using the parametric approach of Fryer (1991), we chose a simpler approach and calculated the nonparametric replication estimate of dispersion (McCullagh and Nelder 1989, p. 127). This estimator calculates, for each length class, the variability over the 15 hauls of the proportion of that length class's catch taken by the experimental codend. Thus, it takes into account both overdispersion and between-haul variation. The replication estimates were $\hat{\sigma} = 1.36$ and $\hat{\sigma} = 1.46$ for the diamond mesh and square mesh codends, respectively. Using these values to correct the standard errors and hypothesis tests again does not change any of the above inferences.

The individual l_{50}'s decreased slightly, although not significantly,with increased catch. Codend catch sizes in this study were low to medium with respect to commercial catches and so the chance of detecting a significant effect of catch size was limited. Also, the limited underwater visibility prohibited complete monitoring of the codends and it is possible that some of the hauls included in the analysis should have been omitted. Inclusion of ''bad'' hauls would contribute to masking of catch size or haul duration effects and add to the between-haul variability noted above. As mentioned earlier, two hauls were omitted from analysis due to severe problems. Of the 30 used, several were noted as having irregularities in their deployment but these were not of a particularly unusual nature and so removing those hauls from the analysis would have been an extremely subjective decision.

The separator section did not function as intended and we feel that it would be very difficult to rig so as to ensure an equal split of fish into the two codends. A full-length vertical separator panel might perform better but it would be very tricky to mount inside a big midwater trawl. Some kind of divided or double trawl system (e.g. Robertson and Shanks 1987) in which the two codends are not connected to the same trawl body, or a covered codend system with a correctly mounted cover, might yield better data.

The difference between the square and diamond mesh codends is not as dramatic here as in the haddock and whiting

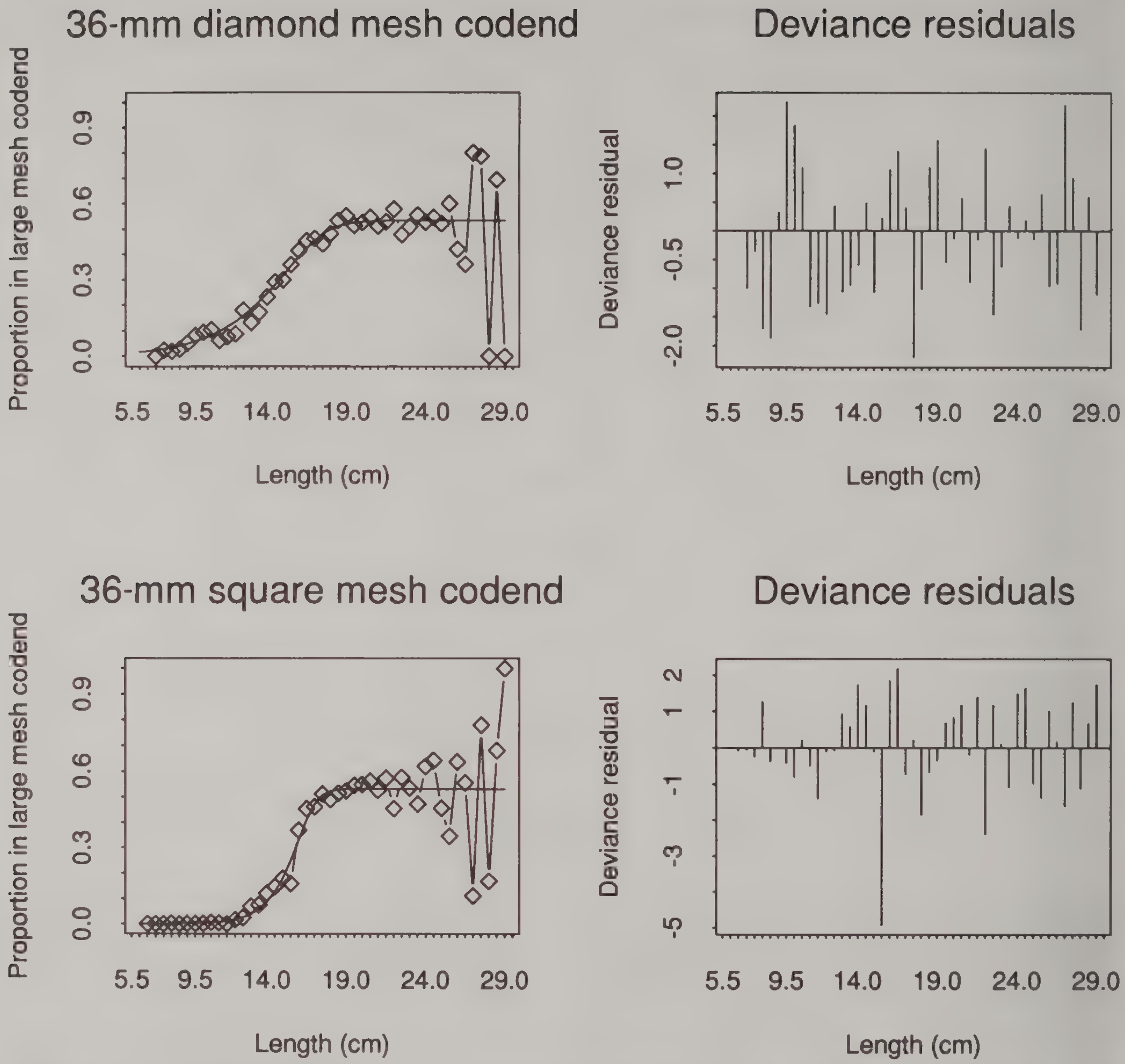


FIG. 8. Plots of the proportion of each length class's total catch taken by the experimental codends for each of the combined data sets, and the residuals from the maximum likelihood fit of the overlaid curve.

studies by Robertson and Stewart (1988). They noted that the number of meshes around the codend and the use of selvedge ropes are both very influential on mesh opening. If such modifications could encourage escape of herring through the codend extension piece, then they could provide further improvements in selectivity. Moreover, it is plausable that opportunitistic escape from the extension piece will be less damaging to the fish then "last ditch" efforts of escape from in front of the catch bulge.

In the Materials and Methods section, it was mentioned that the square mesh codend had on average about a 4% (1–1.5 mm) larger mesh opening than the diamond. This is the same factor by which the square mesh codend's l_{50} exceeded that of the diamond mesh codend, so the difference in l_{50}'s can be attributed to different mesh openings alone. The significant difference in l_{25}'s still holds after increasing the diamond mesh codend's value by 4%. Also, its l_{75} would increase to 17.8 cm which then becomes significantly higher than the estimated 16.9 cm value for the square mesh codend.

Conclusions

The SELECT method of analysis modelled the different fishing efficiencies of the two codends that was observed in the individual and combined haul data, and it showed that asymmetric selection curves best described the combined haul data. Failure to use asymmetric curves would have resulted in the questionable inference that the 36-mm diamond mesh codend retained less large herring than the 36-mm square mesh codend, as evidenced by the l_{75}'s estimated from the symmetric logistic

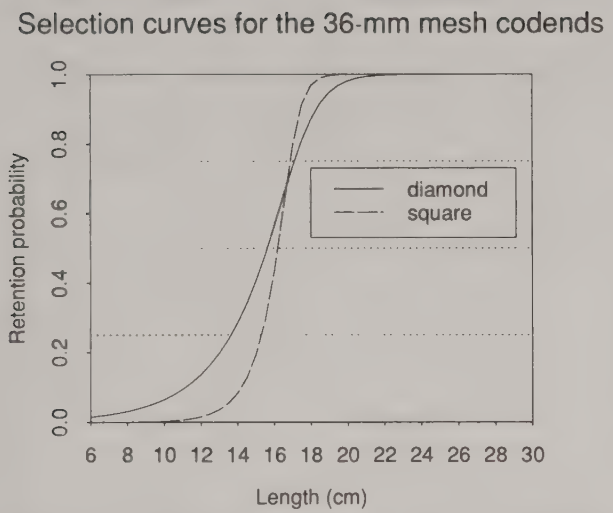


FIG. 9. Asymmetric selection curves for the 36-mm diamond and square mesh codends estimated from the combined data.

curves of 18.4 and 17.4 cm for thse two codends, respectively (Table 5). Both selection curves should have a longer tail to the left of l_{50} than to the right, but because the logistic curve is constrained by symmetry to give equal tails, it overestimated the l_{75}'s, particularly that of the diamond mesh codend.

An increase in the mesh size of diamond mesh codends to 36 mm (whole mesh length) will greatly reduce the catch of small herring (the retention probabilities for 12- and 15-cm fish were estimated to be 14 and 41% for the 36-mm diamond mesh codend; Fig. 9). The loss of large fish will be slight; the probabilities of retention of 18- and 20-cm herring were estimated to be 87 and 98%, respectively. These probabilities apply at the catch rates encountered during this study. The mesh blockage that was observed ahead of the catch bulge suggests that in high catch rate tows the selectivity of the mesh will be impaired in the later part of the tow.

A switch to 36-mm (whole mesh length) square mesh codends will release even more small fish, reduce the number of meshed fish, and may also increase the catch of larger fish. For the square mesh the estimated retention probabilities at 12, 15, 18, and 20 cm were 2, 19, 97, and 100%, respectively. Since most escapes are from the upper side of the codend, constructing the lower panel with diamond mesh or some other strengthening material should not affect selectivity but would reduce the problem of distortion of the square mesh.

Some pelagic herring trawlers have voluntarily begun use of diamond mesh codends with mesh opening larger than the regulated minimum. This study suggests that it is a change that will result in little short-term loss, but has tremendous potential for long-term gains to the fishery. Ongoing research (e.g. Suuronen 1991) is being conducted to see if further improvements in selectivity are attainable, especially when the catch rates are high.

Acknowledgments

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Fertility and Sperm Quality of Virgin and Repeat-Spawning Atlantic Cod (*Gadus morhua*) and Associated Hatching Success

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Trippel, E. A., and J. D. Neilson. 1992. Fertility and sperm quality of virgin and repeat-spawning Atlantic cod (*Gadus morhua*) and associated hatching success. Can. J. Fish. Aquat. Sci. 49: 2118–2127.

Sperm performance of virgin and repeat spawners of Atlantic cod (*Gadus morhua*) was compared. Our results indicate that sperm extracted from either virgin or repeat-spawning male cod exhibit a high capacity (usually >95%) to fertilize eggs at semen:seawater dilutions ranging from 1:1 to 1:100. Fertilization rates at higher dilutions, however, decreased to averages of 47 and 53% at 1:1000, with no statistically significant differences occurring betwen the two types of spawners. Spermatocrit and proportion of sperm cells exhibiting progressive forward motion together accounted for, at most, 14% of the total variability in success of fertilization at semen:seawater dilutions of 1:250, 1:500, and 1:1000. Individuals of both spawner types had immotile sperm, sometimes at high prevalence levels, but these individuals achieved fertiliztion rates comparable with those with high sperm motility. Hatching success of eggs fertilized by virgin males was more variable but, based on mean values, was almost identical to that of repeat spawners. Use of a video camera to record enlarged images of sperm with a haemacytometer grid pattern in the background has permitted the first documented measurements of sperm swimming speeds of a marine teleost fish; the fastest recorded speed was 1000 $\mu m \cdot 30\ s^{-1}$.

On a comparé la performance du sperme de reproducteurs vierges et multifrayes chez la morue franche (*Gadus morhua*). Nos résultats indiquent que le sperme extrait de morue mâle, soit vierge, soit multifraye, présente une forte capacité (généralement supérieure à 95 %) à féconder les œufs à des dilutions semence : eau de mer allant de 1 : 1 à 1 : 100. À des dilutions plus élevées, toutefois, les taux de fécondation baissaient pour atteindre des moyennes de 47 et 53 % à 1 : 1 000, sans différence statistiquement significative entre les deux types de reproducteurs. Le spermatocrite et la proportion de spermatozoïdes capables de se déplacer vers l'avant représentaient, pris ensemble, au plus 14 % de la variabilité totale du succès de fécondation à des dilutions semence : eau de mer de 1 : 250, 1 : 500 et 1 : 1 000. Chez les deux types de reproducteurs, on retrouvait des individus dont le sperme était immobile, avec parfois un niveau élevé de prévalence, mais ces individus obtenaient des taux de fécondation comparables à ceux dont le sperme était très mobile. Le succès d'éclosion des œufs fécondés par des mâles vierges était polus variable et, d'après les valeurs moyennes, était presque identique à celui des géniteurs multifrayes. Grâce à une caméro vidéo enregistrant des images des spermatozoïdes avec en arrière-plan une grille d'hématimètre, on a pu mesurer pour la première fois la vitesse de nage des spermatozoïdes d'un poisson téléostéen marin; la vitesse la plus grande enregistrée était de 1 000 $\mu m \cdot 30\ s^{-1}$.

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Many Northwest Atlantic commercial fish populations have declined over the past 20–30 yr with the current structure of heavily exploited stocks composed predominantly of juveniles and young adults (Scott and Scott 1988). In many stocks of Atlantic cod (*Gadus morhua*), shifts towards maturation at younger ages and smaller body sizes have occurred (Beacham 1983a, 1983b; O'Brien 1989) (Tables 1, 2). The effectiveness of young adults as spawners and their capacity to develop gametes of comparable quality to those of older repeat spawners is therefore of current relevance to assessing a stock's spawning potential.

To date, most of the knowledge concerning the relationship between body size, age, and gamete quality in fishes has been acquired from aquaculture-related research (Crim and Glebe 1990; Kjørsvik et al. 1990). Gamete quality is defined by the characteristics of germ cells which influence fertilization success, egg hatching rate, larval size, and early life survival (the latter two under a strong maternal influence). In some species, the highest quality eggs are produced by the largest and oldest females tested, e.g. Atlantic herring (*Clupea harengus*) (Rosenthal and Hourston 1982), rainbow trout (*Oncorhynchus mykiss*) (Kato and Kamler 1983), and tench (*Tinca tinca*) (Zuromska and Markowska 1984). Other studies indicate that middle-sized females produce the highest quality eggs (Savel'yeva and Shuvatova 1972; Kamler et al. 1982) and, from a study on bream (*Abramis brama*), the smallest females produce the highest quality eggs (Kuznetsov 1973). However, there have been relatively few studies conducted to determine if sperm quality varies with body size and age of males (Büyükhatipoglu and Holtz 1984; Zuromska and Markowska 1984; Crim and Glebe 1990).

Traditional aquaculture practices have achieved high fertilization rates by the use of high sperm concentration and this has probably led to the assumption that sperm quality is not an important constraint of zygote production and subsequent recruitment in marine populations. It is known, however, that in the marine environment, spawning behavior does not necessarily result in complete fertilization of all eggs released by the female. Four percent of the eggs of the pelagic spawners Atlantic cod, haddock (*Melanogrammus aeglefinus*), and witch flounder (*Glyptocephalus cynoglossus*) recovered in horizontal plankton tows were unfertilized (Markle and Waiwood 1986).

TABLE 1. Percentage of sexually mature 2-, 3- and 4-yr-old male Atlantic cod of NAFO (Northwest Atlantic Fisheries Organization) subdivisions 4T, 4Vn, 4Vs, 4W, and 4X from 1959 to 1979. Source: Beacham (1983a, 1983b). Although some values may be subject to criticism (Halliday 1987), the general trend towards earlier maturity is evident. A similar trend was observed among females.

Subdivision	Age (yr)	1959–64	1965–69	1970–74	1975–79
4T	2	0	0	3.0	0.7
	3	1.7	1.5	10.5	15.4
	4	17.6	30.0	42.6	68.6
4Vn	2	0	0	0	21.1
	3	1.6	0	5.4	57.1
	4	23.2	48.0	50.6	81.4
4Vs	2	0	25.0	13.2	15.2
	3	2.5	75.0	40.0	62.9
	4	10.4	78.3	80.1	91.7
4W	2	0.7	7.4	16.1	17.5
	3	5.0	25.3	51.7	65.6
	4	26.3	48.6	82.8	89.3
4X	2	0	0	15.3	21.1
	3	16.2	8.6	59.5	56.3
	4	29.3	72.7	83.4	81.7

TABLE 2. Median age and length at sexual maturity of male Atlantic cod of NAFO subdivisions 4T, 4Vn, 4Vs, 4W, and 4X from 1959 to 1979. Source: Beacham (1983a, 1983b). Although some values may be subject to criticism (Halliday 1987), the general trend towards earlier maturity at smaller sizes is evident. A similar trend was observed among females.

Subdivision	1959–64	1965–69	1970–74	1975–79
Median age at sexual maturity (yr)				
4T	4.96	4.55	4.01	3.58
4Vn	5.58	4.79	4.17	3.08
4Vs	5.43	2.40	3.07	2.72
4W	4.69	3.72	2.94	2.67
4X	4.76	3.69	2.83	2.78
Median length at sexual maturity (FL, cm)				
4T	45.4	48.4	41.9	38.6
4Vn	51.8	41.1	42.6	36.3
4Vs	47.3	42.3	38.5	37.6
4W	46.0	43.5	39.3	37.2
4X	57.1	49.2	45.7	44.7

This is likely an underestimate, as unfertilized eggs typically sink to the ocean bottom whereas fertilized gadid eggs remain in suspension. Autumn-spawning cod along the coast of Nova Scotia have at times exhibited low egg fertilization rates (McKenzie 1940). The essential difference between natural and artificial spawning is the dilution of sperm by seawater and this factor could affect fertilization rates.

Two characteristics of semen that are commonly considered to be reliable indicators of male reproductive potency are spermatocrit and sperm motility (Daye and Glebe 1984; Munkittrick and Moccia 1987). Spermatocrit is a measure of the percentage of the total volume of semen occupied by sperm; high spermatocrit should yield high fertilization rates because of the higher density of sperm per unit volume of milt (Bouck and Jacobson 1976). High sperm motility and its associated greater fertilization range should be positively correlated with fertilization success. Fast-swimming sperm are more likely to encounter an egg's micropyle than slow-swimming sperm.

We designed an experiment using cod to test the followng hypotheses: (i) egg fertilization rates decrease in seawater diluted mixtures of semen, (ii) sperm of first-time spawning males (referred to subsequently as ''virgins'') fertilize a lower number of eggs than sperm of large repeat spawners over a gradient of eight semen:seawater dilutions (1:1–1:1000), (iii) spermatocrit and sperm motility vary with male reproductive experience and these sperm characteristics are associated with egg fertilization rates, and (iv) zygotes fertilized by sperm of virgin spawners exhibit lower hatching rates than those fertilized by repeat spawners.

Methods

Experimental work was conducted at the Biological Station in St. Andrews, New Brunswick, Canada, using cod of Scotian Shelf origin that have been held in captivity for 3–10 yr. These fish had been maintained on a mixed diet of herring and squid (*Illex illecebrosus*).

Immature cod, monitored each year, were observed to attain sexual maturity for the first time in 1991 and were categorized as virgin spawners (range 57–65 cm fork length (FL), 2.1–3.0 kg body weight, and condition factor 0.97–1.18). Larger, reproductively experienced cod (range 85–99 cm FL, 6.8–12.6 kg, and condition factor 1.00–1.34) were approaching breeding condition for approximately the eighth year while in captivity and were categorized as repeat spawners. Although the experimental design contrasts fertility of virgin and repeat-spawning males, it should be noted that the virgins used in this experiment reflect the higher end of the maturity size segment of first-time spawning males in the wild (Table 2).

Fertilizations were conducted on March 7, 1991, which, based on observations in previous years, approximates the middate of spawning. The spawning period in 1991 spanned February 8 – March 23. Sperm of nine virgin and five repeat-spawning males were used to fertilize eggs of a virgin female (62 cm FL, 2.4 kg, and condition factor 1.01). To avoid the use of semen of nonspawning males, fish used in the experiment were stripped 2–3 wk earlier and they had the opportunity to engage in active spawning while in captivity, as was evident by fertilized eggs in tanks (Munkittrick and Moccia 1987).

Each fish was anaesthetized using tricaine methanesulphonate (MS222 at 1:20 000 dilution), the external genital duct region was wiped dry, and gametes were collected while slight pressure was applied along the abdominal cavity towards the genital pore. The first portion of the male ejaculate was usually watery and was discarded. Extracted gametes were stored in individually labelled glass beakers on crushed ice. Fork length (±0.5 cm) and body weight (virgins ±5 g; repeat spawners ±100 g) were recorded for each fish.

Fertilizations were conducted at dilutions of semen:seawater of 1:1, 1:5, 1:10, 1:25, 1:100, 1:250, 1:500, and 1:1000. Semen dilutions specific to a male were started by placing a 0.04-mL aliquot of semen in each of eight, uniquely labelled plastic dishes. To make the most concentrated sperm suspension (1:1 dilution), 0.04 mL of seawater (6°C) was added to the semen in the appropriately labelled dish. Semen and seawater were then stirred with a glass rod for six revolutions (total time ~3 s) and 0.25 mL of eggs (~100 eggs) was added immediately. The eggs, semen, and seawater were left in the dish for 1 min, during which time they were stirred six times, and then poured onto a 300-μm-mesh screen to remove excess sperm. Eggs were returned to the dish, to which 10 mL of seawater was added.

The same procedure was used for the remaining seven dilutions in which 0.2, 0.4, 1, 4, 10, 20, and 40 mL of seawater was added to 0.04 mL of semen, giving a range of dilution of 1:5, 1:10, 1:25, 1:100, 1:250, 1:500, and 1:1000. The experimental design incorporated random ordering of males through time and the entire fertilization series for 14 males was carried out in 5 h. The 112 dishes containing these eggs were maintained overnight in a refrigerated room kept at 6°C.

On March 8, approximately 16–22 h after fertilization, magnified images (40×) were recorded using a high-quality video cassette recorder (VCR). From the video tapes (analyzed at a later date), fertilized eggs were identified by the presence of a morula composed of 64–128 blastomeres (Fridgeirsson 1978). Unfertilized eggs were identified by the presence of a clear cytoplasm with no evidence of blastomere division.

Spermatocrit of each male was determined by collecting semen in two nonheparenized tubes and spinning the samples in a centrifuge for 10 min at 7500 rpm. An average value was calculated for each male. Two spermatocrit values specific to a male ranged from 0 to 12% (mean 4%) of one another. We did not measure sperm density directly, but spermatocrit is considered to be a useful predictor of sperm density (Bouck and Jacobson 1976; Munkittrick and Moccia 1987).

Sperm motility of each male was assessed by viewing a sample of semen (dilution 1:500) in a modified Neubauer haemacytometer using a light microscope (magnification 400×). Sperm present in the field of view were videotaped for a duration of 30–75 s (mean = 45 s). The number of immotile sperm in a sample, and whether they were vibrating or not, was documented. Movement of individual sperm cells was traced across the grid pattern of the haemacytometer (200 × 200 μm). The average head length of a sperm cell was 4.34 μm (range 3.17-5.52 μm, $n = 37$) (E. A. Trippel and J. D. Neilson, unpubl. data). Sperm speed was assessed by measuring the distance a sperm travelled (in micrometres) and dividing by the time (in seconds) it was tracked. Times ranged from 3 s for rapid-moving sperm which moved quickly through the field of view to 75 s for slow-moving sperm. These data were used to calculate the average swimming speed (micrometres in 30 s) of sperm for each male. Assessments excluded movement of sperm beneath cover slips caused by convection currents. This phenomenon was easily recognized when it occurred. It is noteworthy that videotaping of sperm began approximately 30 s after sperm were mixed with water to make the 1:500 dilution. In contrast with the relatively brief activity period of salmonid sperm (typically <1 min; Terner 1986), sperm of cod remained highly motile for up to 10 min after activation by water (see also Westin and Nissling 1991). Therefore, the 30-s delay in commencement of sperm observations was unlikely to affect comparative estimates of sperm motility.

After videotaping on March 7, eggs from each of the 1:100 dilutions were placed in labelled incubation trays 12 × 5 × 6 cm, made of fine Nitex mesh and Plexiglas. With respect to paternal size, the incubators were randomly spaced in a shallow tank fed by a continuous flow of seawater of 6°C supplied by multiple sources to ensure constant water temperature throughout the tank. Eggs were exposed to a daily cycle of 12 h light (11 $\mu E \cdot s^{-1} \cdot m^{-2}$) and 12 h darkness. Incubators were checked daily and hatched larvae were removed and enumerated.

Nonparametric statistical methods were employed (Zar 1984, p. 138). The Mann–Whitney U test was used to test for significant differences between virgin and repeat-spawning fish for spermatocrit, proportion of motile sperm, egg fertilization rate, and hatching rate (SPSS 1990). Spearman rank correlation coefficients were calculated to test for significant associations between these variables. Multiple regression analysis was conducted between percent fertilization, spermatocrit, and proportion of sperm that exhibited progressive forward motion on arcsin-transformed data.

Results

At concentrated semen:seawater dilutions (1:1–1:100), sperm of both virgin and repeat-spawning cod exhibited high fertilization rates (usually >95%) whereas fertilization rates decreased for many individuals at less concentrated semen:seawater dilutions (Fig. 1). Virgin and repeat spawners exhibited similar egg fertilization rates at semen:seawater dilutions 1:250 (91 and 81%), 1:500 (70 and 50%), and 1:1000 (55 and 47%) (Table 3). At each dilution, these rates were not significantly different (Mann–Whitney U test, $p = 0.09$, 0.28, and 0.58, respectively).

Spermatocrit was highly variable among both types of males (Table 3). Spermatocrit averaged 47.3 (range 17.5–73.5) for virgins and 59.4 (range 37.5–98.5) for repeat spawners (no significant difference; Mann–Whitney U test, $p = 0.44$). Fertilization rates were not significantly correlated with spermatocrit (dilution 1:250, $r = -0.23$, $p = 0.40$; 1:500, $r = -0.30$, $p = 0.30$; and 1:1000, $r = 0.01$, $p = 0.96$). Male body length and spermatocrit were not significantly correlated ($r = 0.32$, $p = 0.25$) (Fig. 2).

Sperm were characterized as (i) immotile nonvibrating, (ii) immotile vibrating, and (iii) motile, the latter sperm type exhibiting progressive forward movement (Fig. 3). Immotile nonvibrating sperm occurred in the semen of three of 14 males whereas immotile vibrating sperm occurred in eight of the nine virgins and in three of the five repeat spawners (Fig. 3). Immotile vibrating sperm made up a large proportion of the total sperm in nine males.

The swimming speed of an individual motile sperm was constant as it passed through the 200-μm field of view. Virgins were characterized by swimming speeds up to 425 $\mu m \cdot 30\ s^{-1}$ whereas the fastest sperm swimming speed observed,

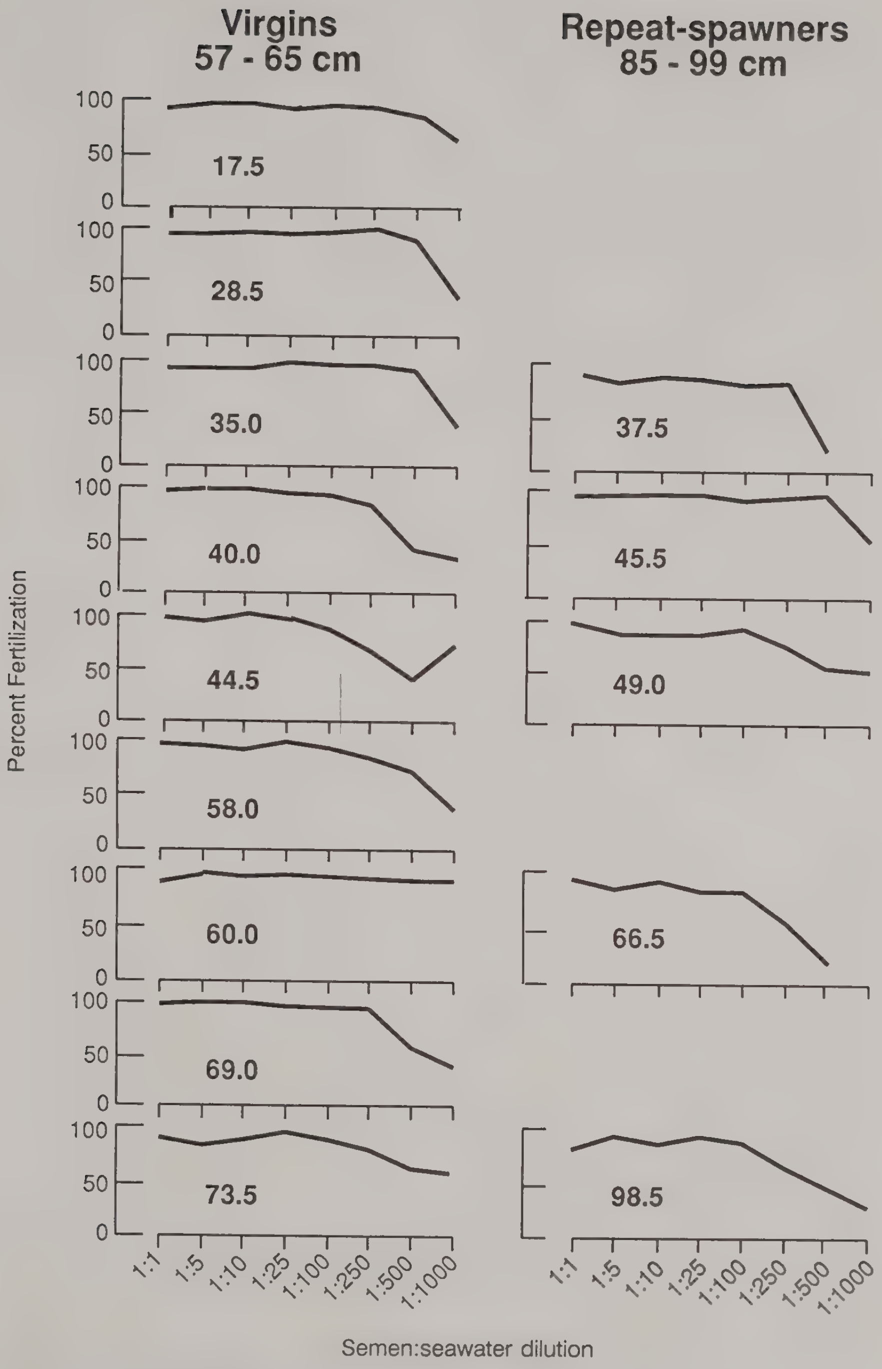

FIG. 1. Percentages of eggs of a virgin female fertilized by nine virgin and five repeat-spawning male Atlantic cod in eight semen:seawater dilutions. Spermatocrit of each male is presented.

1000 $\mu m \cdot 30\ s^{-1}$, was of a repeat spawner (Fig. 3). The average swimming speed of motile sperm of virgins was 71 $\mu m \cdot 30\ s^{-1}$ compared with 79 $\mu m \cdot 30\ s^{-1}$ of repeat spawners (Table 3). Frequency distributions of sperm swimming speeds (Fig. 3) varied considerably among individuals, with their associated variances failing to exhibit homoscedasticity; thus, statistical tests of sperm movement were restricted to nonparametric tests of the percentage of motile cells.

The percentage of motile sperm occurring in virgin and repeat spawners was not significantly different (Mann–Whitney U test, $p = 0.11$) (Table 3). Proportion of motile sperm and body length was not significantly correlated ($r = 0.48$, $p = 0.09$). Proportion of motile sperm did not correlate with egg fertilization rates among the 14 males ($r = -0.34$, $p = 0.22$ (1:250); $r = -0.38$, $p = 0.18$ (1:500); and $r = 0.22$, $p = 0.46$ (1:1000)). Three virgin males having only immotile sperm

TABLE 3. Body size characteristics, spermatocrit, percentage of motile sperm, and mean sperm swimming speeds of virgin and repeat-spawning male Atlantic cod of Scotian Shelf origin. Percentages of eggs fertilized and hatched from a virgin female (62 cm FL) fertilized by sperm of 14 males on March 7, 1991, are also presented for a gradient of semen:seawater dilutions. CF = condition factor (body weight/(fork length)^3) × 100, SE = standard error, N/A = not available. Individuals are ordered by increasing spermatocrit by spawning type.

					Sperm swimming speed (μm·30 s^{-1}) (mean ± SE)			Percent eggs fertilized at semen dilution:				Percentage of total hatch by day for eggs fertilized at semen dilution 1:100					
FL (cm)	Body weight (kg)	CF	Spermatocrit	Percentage of motile sperm	Immotile and motile sperm combined	Motile sperm	No. of sperm (immotile and motile)	1:250	1:500	1:1000	Percent eggs hatched March 20–24	Mar. 20	Mar. 21	Mar. 22	Mar. 23	Mar. 24	No. of larvae hatched
Virgins																	
60	2.25	1.04	17.5	100.0	210 ± 10	210 ± 10	30	97	89	65	43	5.5	16.7	0	55.5	22.2	18
58	2.30	1.18	28.5	0	0	N/A	21	100	92	38	40	10.3	10.3	0	51.7	28.7	29
61	2.50	1.10	35.0	0	0	N/A	34	97	94	43	66	3.3	6.6	9.8	19.6	60.7	61
64	2.55	0.97	40.0	17.9	13 ± 3	48 ± 12	56	84	44	39	N/A						
62	2.40	1.01	44.5	7.2	7 ± 3	10 ± 0	28	73	40	71	71	0	0	0	38.1	61.9	42
65	3.00	1.09	58	23.1	23 ± 3	13 ± 2	26	90	77	41	58	0	0	0	33.3	66.7	39
63	2.60	1.04	60	89.2	32 ± 9	54 ± 10	41	99	N/A	94	93	0	0	0	17.5	82.5	63
57	2.10	1.13	69	0	0	N/A	32	99	61	44	63	0	0	0	20.0	80.0	55
63	2.55	1.02	73.5	23.8	21 ± 4	91 ± 19	21	84	65	63	60	2.3	0	13.6	29.5	54.6	44
Mean (SE)																	
61 (0.8)	2.47 (0.08)	1.06 (0.02)	47.3 (6.0)	29.0 (12.1)	34 (21)	71 (28)		91.3 (2.9)	70.3 (7.1)	55.3 (6.0)	61.8 (5.9)	2.7 (1.2)	4.2 (2.1)	2.9 (1.8)	33.2 (4.8)	57.2 (7.1)	
Repeat spawners																	
93	10.4	1.29	37.5	30.8	53 ± 19.1	171 ± 111	26	84	24	N/A	68	7.7	1.9	17.3	21.2	51.9	52
99	12.6	1.30	45.5	9.1	55 ± 17.3	12 ± 0	33	96	100	53	N/A						
85	8.2	1.34	49.0	100.0	70 ± 2.7	69 ± 5	30	78	54	51	N/A						
88	6.8	1.00	66.5	67.4	43 ± 3.4	64 ± 3	61	61	21	N/A	55	9.5	4.8	0	35.7	50.0	42
98[a]	10.2	1.08	98.5	100.0	78 ± 1.8	77 ± 3	34	85	53	38	66	5.7	0	0	20.8	73.5	53
Mean (SE)																	
93 (2)	9.4 (0.9)	1.20 (0.06)	59.4 (9.7)	71.5 (16.3)	59 (11)	79 (23)		80.8 (12.7)	50.4 (3.8)	47.3 (3.3)	63.0 (3.2)	7.6 (0.9)	2.2 (1.1)	5.8 (4.7)	25.9 (4.0)	58.5 (6.1)	

[a] Experimental fish died several hours before the experiment began with no clear evidence available for its cause of mortality. The results of this individual were included, as their removal did not change the conclusions of the study.

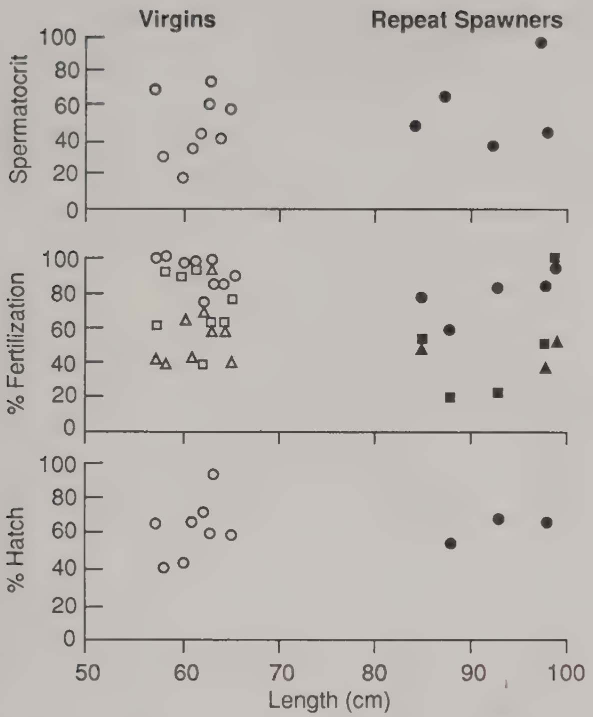

FIG. 2. Associations between body length of cod and spermatocrit, percent egg fertilization rates at semen:seawater dilutions 1:250 (circles), 1:500 (squares), and 1:1000 (triangles), and egg hatching rates for eggs fertilized at a semen:seawater dilution of 1:100.

yielded fertilization rates similar to those reported for virgin and repeat-spawning males with motile sperm (Table 3). Spermatocrit and proportion of motile sperm were not significantly correlated ($r = 0.26$, $p = 0.36$). Spermatocrit and proportion of motile sperm explained, in total, 13.8, 14.2, and 12.9% of the variation in percent fertilization at dilutions 1:250, 1:500, and 1:1000, respectively.

Hatching commenced 12 d after fertilization (March 20) for eggs fertilized by four of eight virgins and all repeat spawners (Table 3). Eggs fertilized by the other four virgins commenced hatching 15 d after fertilization (March 23). Hatching was completed on March 24 for all crosses. Hatching success was more variable for eggs fertilized by virgins (range 43–93%, CV = 23) relative to repeat spawners (55–68%, CV = 9), but there was no significant difference in the mean hatching success rates which were 62% for virgins and 63% for repeat spawners (Mann–Whitney U test, $p = 0.78$). Hatching rates for all males pooled were not significantly correlated with male body length ($r = 0.22$, $p = 0.46$), spermatocrit ($r = 0.44$, $p = 0.14$), and proportion of motile sperm ($r = 0.10$, $p = 0.73$) (Fig. 2). Percent fertilization and percent hatching rates were not significantly correlated among males ($r = -0.23$, $p = 0.45$ (1:250); $r = -0.29$, $p = 0.36$ (1:500); and $r = 0.55$, $p = 0.10$ (1:1000)).

Discussion

Male Potency

Our results indicate that sperm extracted from either virgin or repeat-spawning male cod exhibit a high capacity (usually >95%) to fertilize eggs at semen:seawater dilutions ranging from 1:1 to 1;100. At higher dilutions (1:250, 1:500, and 1:1000), however, fertilizing capacity decreased for both virgins and repeat spawners, with no significant differences occurring between the two types of spawners. Virgin males of other fishes also have exhibited high fertilization capacity; however, these studies were conducted in concentrated sperm media (Zuromska and Markowska 1984; Fredrich et al. 1987). To our knowledge, only one study has examined the relative potency of virgin males under simulated natural spawning conditions (Hutchings and Myers 1988).

Our observations indicate, as do those by a minority of other workers on seven species (Table 4), that neither high spermatocrit (a correlate of sperm density) nor high sperm motility is always essential for successful fertilization. The lack of predictive capabilities of spermatocrit and sperm motility suggests that other features of sperm are likely also critical to fish sperm fertilizing potential, such as the chemical composition of the semen (Gilkey 1981; Jamieson 1991, p. 248).

Immotile sperm which were vibrating were present in the semen of most individual cod in our study (Fig. 3). Despite this, sperm of individuals with immotile sperm fertilized eggs at a level similar to males having exclusively motile sperm (Table 3). Several other studies, as reviewed by Scott and Baynes (1980), confirm that immotile sperm are capable of fertilizing eggs, although in these other studies, the semen was either taken from a dead fish (Okada and Ito 1955), stored undiluted at 2°C under O_2 for 23 d (Stoss et al. 1978), or thawed after a period at −196°C (Truscott and Idler 1969).

Changes in Spermatocrit with Age and Length in Fishes

No association between spermatocrit and male reproductive experience was found in our study, but this is not necessarily representative for teleosts as a whole as outlined for five species (Table 5). In a study on rainbow trout in which the same individuals were monitored as virgins (2-yr-olds) and as repeat spawners (3-yr-olds), it was found that sperm density of virgins decreased more rapidly as the spawning season progressed (Büyükhatipoglu and Holtz 1984). Small virgin Atlantic salmon (*Salmo salar*) parr (nonanadromous) had a spermatocrit of 49 compared with 28 for older anadromous males, a near 1.75-fold difference, and there was a 1.55 difference in sperm density (30.4 million versus 19.6 million·mm^{-3}). Evidence that middle-aged males have the highest spermatocrit is presented for several species. Specifically, for Baikul omul (*Coregonus autumnalis migratorius*), sperm density (in cubic millimetres) increased from 4.13 million for males ages 6–7 yr to 6.9 million at age 9 to 8.5 million at ages 10–11 and then decreased at ages greater than 11 to 6.9 million (Khodzher 1981). The density of sperm for rainbow trout decreased with increasing age (Babushkin 1974). Near the end of the spawning season, older Issyk-Kul chebachok (*Leuciscus bergi*) had lower concentrations of sperm than younger fish, although high variability was observed in the volume of ejaculate and in sperm concentration of males of identical size (Turdakov 1965). As in our study of cod, an increase in fish size and reproductive experience did not affect sperm density for Azov roach (*Rutilus rutilus heckeli*) (Zhukinskiy 1965).

A New Technique of Assessing Sperm Motility

The problems of accurately measuring sperm motility are far more complicated than those for spermatocrit and sperm density, particularly because of the limited time during which sperm

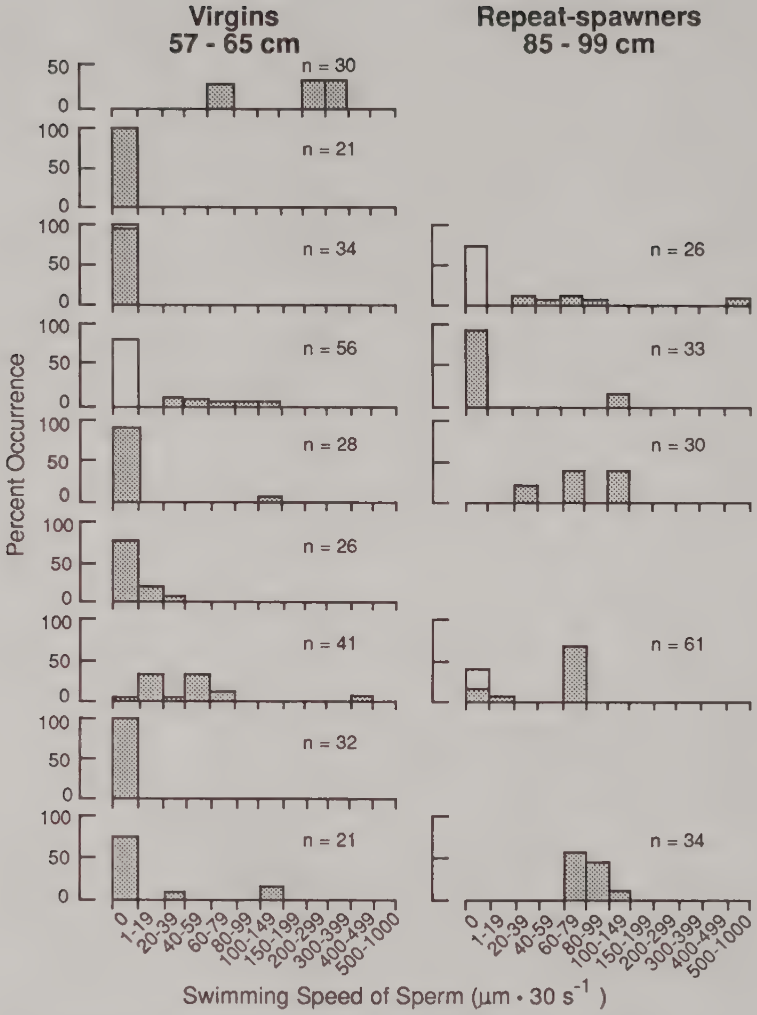

FIG. 3. Percent occurrence of sperm having different swimming speeds for virgin and repeat-spawning male Atlantic cod. The open bars represent sperm which were immotile and not vibrating whereas the shaded bars represent immotile vibrating and motile sperm. Individuals are ordered in the same fashion as in Fig. 1. *n* = number of sperm.

are active. For this reason, sperm motility has not been assessed consistently in different studies, and comparison of results is difficult (Billard and Cosson 1992).

Ranked scores of general motility are commonly used, but researchers have employed different rank ranges: 1–3 (Moccia and Munkittrick 1987), 1–5 (Wilcox et al. 1984), 1–7 (Zuromska and Markowska 1984), and 1–10 (Munkittrick and Moccia 1987). Another criterion has been the duration of sperm motility, i.e. when all (or most) of the sperm stop exhibiting progressive forward movement (Rutter 1902; Scheuring 1928; Buss and Corl 1966; Duplinsky 1982; Zuromska and Markowska 1984; Westin and Nissling 1991). This latter method has its limitations, as duration does not reflect individual variation among spermatozoa. Other approaches to assessing sperm motility include categorizing sperm as immotile, motile progressive, motile circling, and the proportion of each of these types (Terner 1986). These different types of evaluations make it difficult to compare sperm motility among species and to assess the biological significance of this reproductive trait.

Our technique of using a video recorder of enlarged images of sperm against a haemacytometer grid pattern in the background makes it possible to measure sperm swimming speed. The ability to scan and reexamine the permanent record allows much greater flexibility in the analysis of movements of individual sperm cells. It is also possible to determine the ability of individual sperm to sustain motility by following them over the slide and this could supplement the measures of sperm velocity. Our findings on cod indicate that a sperm cell swimming at 75 $\mu m \cdot 30\ s^{-1}$ (mean of 14 males) would require ~14 min to travel to the opposite side of a cod egg 13 mm in diameter. Presumably, the lengthy period of motility of cod sperm (mean values up to 16 min in Baltic cod; Westin and Nissling 1991) would still enable a sperm to enter the micropyle of an egg after progressing the distance. However, the slow swimming speed of many of the other sperm cells measured indicates that sperm would have to come into contact with an egg in close proximity to its micropyle to achieve self-propelled fertilization. It is likely that the motion of water along the egg's

TABLE 4. Effects of spermatocrit, sperm density, and duration of sperm motility on egg fertilization rates of wild and cultured teleost fishes.

Species	Spermatocrit	Sperm density	Sperm motility	Fish	Dilution	Reference
Atlantic salmon (*Salmo salar*)	No effect	No effect	No effect	Wild	Dry fertilization	Daye and Glebe 1984
Dog salmon (*Oncorhynchus keta*)			Positive, i.e. immotile sperm from dead fish fertilized 46% of eggs relative to 96% for motile sperm from live fish		Dry fertilization	Okada and Ito 1955
Rainbow trout (*Oncorhynchus mykiss*)	No effect	No effect	No effect	Cultured	Dry fertilization	Moccia and Munkittrick 1987
		Positive late in reproductive season	Positive		200 000 sperm·egg^{-1}	
			Positive, i.e. high abundance of immotile sperm reduces fertilization rate	Cultured	Dry fertilization	Levanduski and Cloud 1988
Atlantic cod (*Gadus morhua*)			No effect, i.e. in a few cases after cyropreservation, motile sperm do not fertilize eggs	Cultured	Dry fertilization	Mounib et al. 1968
Atlantic herring (*Clupea harengus*)		Positive		Wild	1:1 → 1:512 semen: seawater dilution or $0.57 \times 10^6 \rightarrow 258 \times 10^6$ sperm·mL^{-1}	Rosenthal et al. 1984
Common carp (*Cyprinus carpio*)		Positive	Positive	Cultured	1:30 → 1:250 semen: seawater dilution	Koldras and Mejza 1983
			No effect, i.e. after cyropreservation, motile sperm do not fertilize eggs	Cultured	Dry fertilization	Kossman 1973
Striped mullet (*Mugil cephalus*)		Positive	Positive		Dry fertilization	Fedulina 1989

surface plays a major role in influencing sperm : egg micropyle encounter rates. Similarly, the significance of egg size, micropyle location, sperm velocity, and the duration a sperm remains motile has been commented on for rainbow trout (Billard and Cosson 1992). Despite the relatively fast velocity of rainbow trout sperm (~60-fold faster then cod), its brief longevity restricts its self-propelled fertilization range.

Changes in Sperm Motility with Age and Length in Fishes

Duration of sperm movement in relation to a male's age and length has been assessed previously, yet no consistent pattern has emerged (Table 5). Scheuring (1928), working on rainbow trout, demonstrated an increase in the duration of progressive motion of sperm over the first few years of reproductive activity which was then followed by a decrease. In a detailed experiment, also on rainbow trout, Büyükhatipoglu and Holtz (1984) found that first- and second-time spawners produced sperm with similar mean values of motility; however, variability was greater among first time spawners. The sperm of Atlantic salmon parr had a longer duration of motility (1.42-fold) than that of sea-run males at pH 7.0 (Daye and Glebe 1984). No change in duration of sperm motility was detected in Baikal omul in the age range 6–14 yr (Khodzher 1981).

Sperm:Egg Association in Cod

Cod are pelagic spawners, with large spawning aggregations occurring off the ocean bottom at depths ranging from 50 to 400 m (Brawn 1961). The sperm:seawater dilutions at which fertilization occurs in the cod's natural habitat are thus important in the interpretation of our findings. Observations made in indoor tanks have shown tight nuptial activities between pairs of breeding fish (Brawn 1961). The two fish align their genital pores and swim in close proximity to one another, so that release of sex products would yield a relatively concentrated solution.

Sizes of the male and female that join in spawning might be a factor in breeding success, where close alignment of fish of the same or vastly different sizes could influence the composition of the sperm, egg, and water environments in which sex products are mixed (Kjesbu 1989). To what extent males and females join in spawning based on their size needs to be examined. Based on the time that cod sperm remain active and the fact that immotile sperm fertilize eggs, the mass expulsion of sex products by a large number of females and males may result in the indiscriminate fertilization of an egg by a male that did not participate in a specific courtship. Furthermore, the long-term capacity for cod eggs kept in seawater to become fertilized (50% after 2 h) (Kjørsvik and Lønning 1983) suggests that polygamy may occur in this species.

TABLE 5. Age, length, spermatocrit, sperm density, and duration of sperm motility in wild and cultured teleost fishes.

Species	Age (yr)	Length (cm)	Spermatocrit (sperm density)	Sperm motility		Fish	Reference
Atlantic salmon (*Salmo salar*)	Precocious male parr		Spermatocrit = 49 (30.4 × 10^6 sperm·µL^{-1})	85 s	pH 7.0	Wild	Daye and Glebe 1984
	Sea-run males		Spermatocrit = 28 (19.6 × 10^6 sperm·µL^{-1})	60 s			
Rainbow trout (*Oncorhynchus mykiss*)	Age 1 (virgins)			33 s		Cultured	Scheuring 1928
	4			51			
	5			65			
	7			45			
	Age 2 (virgins)	30.2	(11.2 × 10^6·mm^{-3})	30.2 s		Cultured	Babushkin et al. 1971
	3	39.6	8.3	26.3			
	4	49.3	7.4	36.3			
	Age 2 (virgins), 300 g		Sperm density similar between seasons; however, density declines quickly in virgins as season progresses	Week 1	13.2 s	Cultured	Büyükhatipoglu and Holtz 1984
				2	17.3		
				4	20.0		
	Age 3 (1 yr of experience), same individuals			1	12.8 s		
				2	15.4		
				4	14.6		
Baikal omul (*Coregonus autumnalis migratorius*)	Age 6–7	33.7–34.6	(4.13 × 10^6·mm^{-1})			Wild	Khodzher 1981
	9	36.5	6.90	Mean = 36.2 s; little change with age			
	10–11	37.0–38.1	8.50				
	> 11	39.3	6.90				
Issyk-Kul chebachok (*Leuciscus bergi*)		40.0–99.9	Near the end of the spawning season, larger fish have lower concentrations of sperm than smaller fish			Wild	Turdakov 1965
Azov roach (*Rutilus rutilus heckeli*)	Not provided		No connection between the age and size of males and sperm concentration				Zhukinskiy 1965

Implications for Management

Any differential gamete quality with reproductive experience, whether of male or female, would have management implications for any stock whose age and size composition were truncated by fishing (e.g. see Leaman 1991). The measured spawning stock biomass would not then be a reliable quantitative indicator of spawning potential and would have to be subject to age- and size-dependent weighting for gamete quality. For example, evaluating the male contribution of spawning stock biomass might involve multiplying the abundance of males in each size group by their reproductive potential (testes weight × sperm density × capacity of sperm to fertilize eggs). Our results indicate that, for Atlantic cod, there are no such size-related differences for males although the observed high variability in fertilization rates indicates the difficulty in establishing a size-specific potency potential that may be included in such an equation.

Examining to what extent early maturity limits reproductive success in cod is currently of considerable relevance, considering the current age and size structures of many cod stocks in the northwest Atlantic. Over a 20-yr period, 1959–79, drastic changes occurred in the maturation schedules of cod, during which cod began maturing at younger ages and smaller sizes (Tables 1, 2). Sexual maturity among males for four NAFO subdivisions has progressed such that a proportion of the males of all stocks by 1979 were exhibiting sexual maturity at age 2 yr. In some cases, the proportion of mature 2-yr-olds attained 21%. As well, 3- and 4-yr-old males exhibited advanced sexual maturity (Table 1) and this was reflected in the decreases in median age at sexual maturity for these stocks, for example, a decrease from 4.76 to 2.78 yr in the 4X stock (Table 2). Furthermore, concurrent with younger ages at first reproduction, fish were maturing at smaller sizes. In area 4Vn, median length at sexual maturity of male cod was 36.3 cm from 1975 to 1979, 30% shorter than in the 1959–64 period.

Because the virgin males of our study were much larger than many of the virgin cod in the northwest Atlantic, it is likely that our findings are restricted to a specific proportion of the maturity schedule in the wild. It would be significant to conduct further studies of gamete quality on virgin males 35–55 cm, which would extend our findings to the lower threshold of sexual maturation observed for this sex.

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Temporal and Spatial Dynamics in Riverbed Chemistry: The Influence of Flow and Sediment Composition

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To characterize the nutrient pool in the riverbed of an unregulated river in western Canada and identify factors controlling spatial and temporal variability, nitrogen and phosphorus concentrations in open water, porewater, and sediment-exchangeable pools were monitored in the Pembina River, Alberta, at three sites that differed in sediment composition (cobble, sand, and fine sediments). Comparison of porewater chemistry for three years showed that interannual variation was related to discharge rate (22, 87, and 68 m^3/s for May–November 1988, 1989, and 1990, respectively) and changes in the size composition of the bottom sediments. However, within-year variations in riverbed chemistry were not correlated with either flow or current velocity. These results suggest that large-scale interannual changes in flow act as a set-point mechanism, defining the particle size composition and chemistry of the riverbed; flow changes of short duration had no predictable effect on riverbed chemistry. Our finding on the highly dynamic nature of riverbed chemistry has important implications for benthic productivity and elemental fluxes between surface waters and the riverbed because dramatic changes in riverbed chemistry can occur in the span of a year even without a flushing scour.

Afin de caractériser le pool d'éléments nutritifs du lit d'une rivière non régulée, dans l'ouest du Canada, et afin de déterminer quels facteurs contrôlent la variabilité dans l'espace et dans le temps, on a mesuré à intervalles réguliers la concentration en azote et en phosphore des eaux libres, de l'eau interstitielle et de la partie des sédiments qui participe à des échanges. Trois stations ont été choisies dans la rivière Pembina (Alberta); elles diffèrent par la composition des sédiments (gravier, sable et sédiments fins). La comparaison sur trois années de la chimie de l'eau interstitielle a montré que les variations d'une année à l'autre sont en fonction du débit (22, 87 et 68 m^3/s en mai–novembre 1988, 1989 et 1990, respectivement) et en fonction des variations granulométriques des sédiments. Toutefois, les variations observées dans la chimie du lit de la rivière au cours d'une même année, n'étaient pas en corrélation avec l'écoulement ni la vitesse du courant. Ces résultats portent à penser que les importantes variations de l'écoulement d'une année à l'autre constituent le mécanisme enclencheur, qui définit la composition granulométrique ainsi que la chimie du lit de la rivière; les variations d'écoulement de courte durée n'ont pas d'effet prévisible sur la chimie du lit de la rivière. Notre observation du caractère fortement dynamique de la chimie du lit de la rivière a d'importantes incidences sur la productivité en milieu benthique et sur les flux d'éléments entre l'eau de surface et le lit de la rivière, du fait que des modifications spectaculaires de la chimie du lit peuvent se produire à l'intérieur d'une même année sans qu'il se produise d'affouillement par effet de chasse.

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Temporal and spatial patterns in lake-bottom chemistry have been well documented, particularly with regard to their importance in nutrient cycling (Mortimer 1941, 1942; Golterman 1984). In contrast, much less is known about temporal patterns in river chemistry, particularly the chemistry of riverbed sediments. Observations that stream sediments regulate nutrient concentrations in the overlying water (Klotz 1988), have greater bacterial biomass than stream waters (Meyer et al. 1987), trap and process organic matter (McDowell and Fisher 1976; Lush and Hynes 1978; Dahm 1981) and are a major source of nutrients to aquatic plants in rivers (Pringle and Bowers 1984; Chambers et al. 1989) indicate that bottom sediments play an important role in stream metabolism. However, despite their importance, relatively few studies have examined riverbed nutrient dynamics. Moreover, among those that have, the focus has been on exchanges between the streambed and lateral extensions of the hyporheic zone (e.g. Ford and Naiman 1989; Triska et al. 1989; Triska et al. 1990; Valett et al. 1990). These studies have shown that for small, often intermittent streams, summertime changes in dissolved oxygen, dissolved organic carbon, and/or ammonium concentrations in the streambed and across the riparian zone are largely due to shifts in the depth of the groundwater – surface water interface as a result of changes in instream flow. Little is known of nitrogen and phosphorus dynamics in bottom sediments, particularly for larger rivers, and over time periods longer than the summer months. Yet knowledge of temporal dynamics in riverbed chemistry is critical for predicting benthic productivity and community structure, calculating the magnitude and timing of elemental fluxes to downstream reaches, and modelling nutrient and energy cycling.

The aim of this study was to characterize the nutrient pool in the riverbed of an unregulated river in western Canada and to identify the factors controlling temporal variability in riverbed chemistry. This work forms part of a larger study aimed at establishing nutrient loading and flow criteria to improve water quality and reduce excessive aquatic macrophyte growth in prairie rivers. A 3-yr study of nutrient pools in the Pembina River, Alberta, was undertaken in which open-water, pore-water, and sediment-exchangeable phosphorus and nitrogen concentrations were monitored under a variety of flow regimes at three sites differing in riverbed composition. This allowed us to identify temporal patterns and the factors associated with spatial and temporal variability in riverbed nutrient chemistry.

Methods

Study Site

The Pembina River is a fifth-order stream and a tributary of the Peace–Athabasca river system. It originates in west-central Alberta, Canada, in the Rocky Mountain foothills and flows northeast, joining with the Athabasca River west of Athabasca, Alberta (Fig. 1). The latter flows into the Peace River which eventually drains into the Arctic Ocean through the Mackenzie River. The Pembina River drains 14 330 km^2. Three study sites were selected on the basis of riverbed composition from data collected in a 1986 survey of the river (Chambers et al. 1991). Site I was located approximately 152 km upstream of the confluence of the Pembina and Athabasca rivers. Here, the riverbed was composed of fine sediments (silt and clay); aquatic macrophytes (*Potamogeton pectinatus* and *Potamogeton richardsonii*) were present at depths of <1 m during the low-discharge year (1988), while clams (*Lampsilis radiata*) were present throughout the study. Site II was located 83 km upstream of the confluence. The bottom sediments were composed almost entirely of sand; aquatic macrophytes and clams were absent. Site III was located 27 km upstream of the confluence. The riverbed was composed of gravel/cobble/boulder underlain by sand; aquatic macrophytes and clams were absent. Henceforth, Sites I, II, and III will be referred to as the fine-sediment, sand, and cobble sites, respectively.

At the study sites, the Pembina River averages 75 m in width. Vegetation is typical of the boreal mixedwood region of Alberta (Strong and Leggat 1981) and the area is underlain by Upper Cretaceous bedrock covered by glacial till 10–200 m thick. Climate is continental: mean annual precipitation is 400–

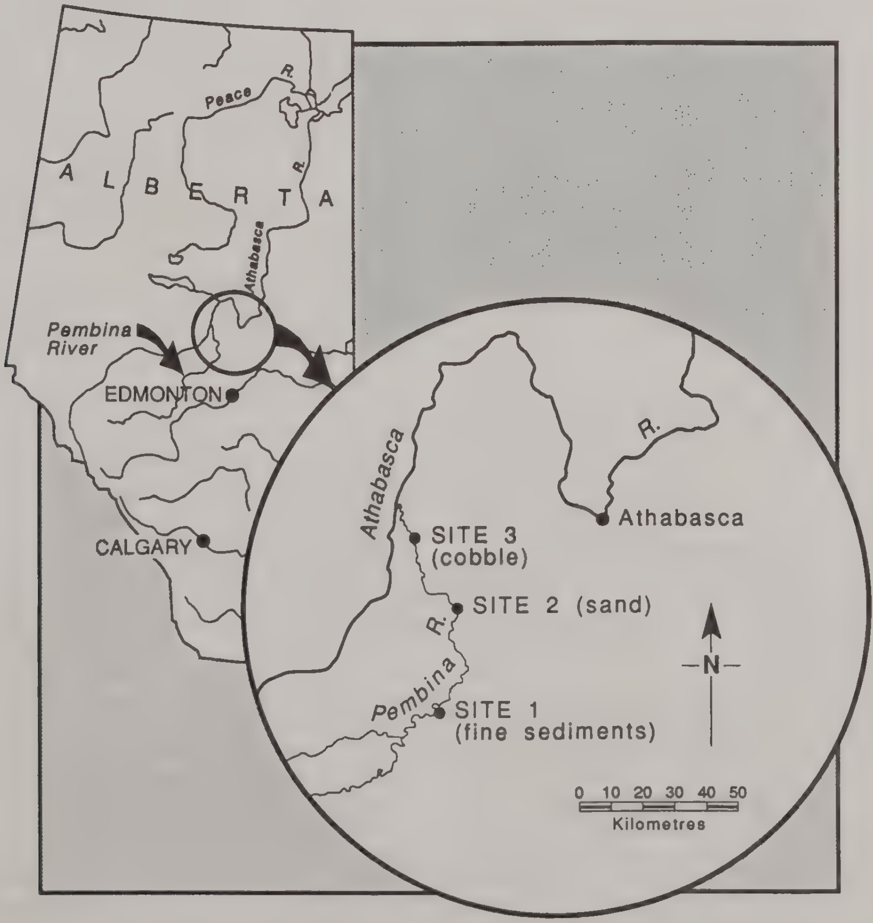

FIG. 1. Map of Alberta, Canada, showing the study sites on the Pembina River.

500 mm and mean annual lake evaporation is 500–600 mm (Fisheries and Environment Canada 1978). Flows are not regulated, averaging 37.1 m^3/s (1962–88) at the sand site, and track the seasonal pattern of late spring snowmelt (May), maximum yearly precipitation in midsummer (July), and minimum yearly precipitation in fall and winter (Environment Canada 1988). Discharge data are not available for the other sites; however, flows are unlikely to differ substantially between sites, as there are no major tributaries feeding the river over the 125-km study reach. The river is typical of freshwater throughout western Canada east of the Rocky Mountains in that it is hardwater with salt concentrations averaging 42, 10.2, 9.9, 2.2, 7.0, and 1.2 mg Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, SO_4^{2-}, and Cl^{-}/L, respectively (P. A. Chambers and E. E. Prepas, unpubl. data).

Sampling Methods

The three sites were visited between May and November on 28, 29, and 25 occasions in 1988, 1989, and 1990, respectively. On each date, open-water samples were collected 15–30 cm below the water surface and placed in Nalgene polyethylene bottles (for phosphorus analyses) or polystyrene containers (for nitrogen analyses). All water samples were stored on ice in coolers and then refrigerated at 4°C in the laboratory until analyzed. Current velocity was measured at each site with a Gurly-Price model 22 current meter 0.1 m below the water surface.

Porewater and sediment samples were collected on seven or eight sampling dates each year. Pore water was sampled with close-interval Plexiglas dialyzers (Hesslein 1976) fitted with biologically inert membranes (Gelman HT-450). The samplers were filled with degassed distilled deionized water and allowed to equilibrate in a closed water bath bubbled with nitrogen gas for at least 4 d prior to use. Two samplers were then inserted side-by-side into the riverbed at each site, ensuring that the same location (within 1 m^2) was maintained throughout the entire study. The samplers were allowed to equilibrate with the pore water for a minimum of 17 d before retrieval (Carignan 1985; Shaw and Prepas 1989). On each sampling date, two samplers were retrieved from each site. Porewater was recovered from the samplers with syringes. Samples were pooled over 5-cm depth increments (i.e. 0–5, 5–10, 10–15, 15–20, and 20–25 cm below the sediment–water interface) and analyzed for soluble reactive phosphorus (SRP; all three years) and Fe^{2+}, NH_4, Ca^{2+}, and dissolved oxygen (DO) in 1989 and 1990. Samples for SRP, NH_4, Ca^{2+}, and Fe^{2+} analysis were injected into glass vials that had been gassed with nitrogen and capped with Wheaton stoppers. Samples for DO analyses were fixed in the syringe following the micro-Winkler method of Burke (1962). All porewater samples were removed from the sampler within 5 min of retrieval to reduce contact with the air and chemical precipitation. The samples were kept in the dark on ice until analyzed. Two sediment cores (25 cm long, 5 cm inside diameter) were collected near each porewater sampler. Within 24 h of collection, the cores were extruded and sectioned into 5-cm slices that were frozen for subsequent analysis. Only the 0–5 cm depth stratum was analyzed in 1988; all five strata (0–5, 5–10, 10–15, 15–20, and 20–25 cm deep) were analyzed in 1989 and 1990. Because of constraints imposed by high flows, it was not possible to collect porewater and sediment samples from every depth stratum on each sampling date.

Analytical Methods

Surface water samples were analyzed for phosphorus (total (TP), total dissolved (TDP), and SRP) and nitrogen (ammonium (NH_4) and nitrite + nitrate (NO_2 + NO_3)). Water samples for phosphorus analyses were analyzed wthin 24 h of collection. Samples for TDP and SRP analyses were filtered through prewashed 0.45-μm HAWP Millipore membrane filters; samples for TP and TDP analyses were digested and analyzed by Menzel and Corwin's (1965) potassium persulfate method. Samples were analyzed for SRP following Murphy and Riley's (1962) molybdenum blue method. Water samples for nitrogen were analyzed within 24 h (NH_4) or 48 h (NO_2 + NO_3) of collection. NO_2 + NO_3 samples were filtered through pre-washed 0.45-μm HAWP Millipore membrane filters. NH_4 and NO_2 + NO_3 were determined with a Technicon autoanalyzer (Stainton et al. 1977). All water analyses were performed in triplicate.

Porewater samples were analyzed for SRP, NH_4, Fe^{2+}, Ca^{2+}, and DO. All samples were analyzed within 24 h of collection. SRP and NH_4 were analyzed on a spectrophotometer following the molybdenum blue method of Murphy and Riley (1962) and the phenol hypochlorite method of Solorzano (1969), respectively. Fe^{2+} was analyzed on a spectrophotometer following the phenanthroline method (American Public Health Association 1985). DO was determined by titration against sodium thiosulfate following the Burke (1962) micro-Winkler method. Ca^{2+} was analyzed by flame emission on a Perkin Elmer (model 3030) atomic absorption flame emission spectrophotometer (American Public Health Association 1985). All porewater samples were analyzed in duplicate.

Sediment samples were analyzed for exchangeable nitrogen and phosphorus on previously frozen sediments that were left to thaw to room temperature. Exchangeable phosphorus was extracted by shaking sediment samples for 16 h with 0.1 N NaOH – 0.1N NaCl (after Williams et al. 1967) and measured spectrophotometrically (Murphy and Riley 1962). Exchangeable nitrogen was extracted by shaking sediment samples for 1 h with 2 M KCl (Bremner 1965) and measured spectrophotometrically as ammonium (Solorzano 1969). Sediment nutrient concentrations are expressed per dry weight of sediment as determined by drying wet sediments to constant weight at 110°C. All sediment chemical analyses were performed in triplicate. Sediment particle size was determined on selected 0–5 cm deep samples following the hydrometric method of Gee and Bauder (1986).

Statistical Methods

Data were analyzed with the Statistical Analysis System (SAS Institute Inc. 1988). Differences in open-water nutrient chemistry between sites were determined by multivariate analysis of variance (MANOVA) for 3 yr of data. Comparisons of porewater and sediment chemistry between sites and depth strata were based on a 2-yr (1989 and 1990) data set and analyzed by MANOVA. Within each site, differences in porewater SRP concentrations between date and depth stratum were determined by ANOVA for 3 yr of data. Comparison of data from all dates and depths showed that porewater and sediment nutrient concentrations varied on average by a factor of 2 for samples collected from peepers or cores positioned side-by-side in the riverbed. These differences were, however, not significant ($P > 0.2$; ANOVA) relative to changes associated with depth or date; adjacent samples were therefore treated as duplicates. Because of differences in compaction of the riverbed, sediment data were only available for three depth strata (0–5, 5–10, and 10–15 cm) at the cobble and fine-sediment sites.

All ANOVA and MANOVA tests were followed by Student–Newman–Keuls (SNK) multiple range tests to identify differ-

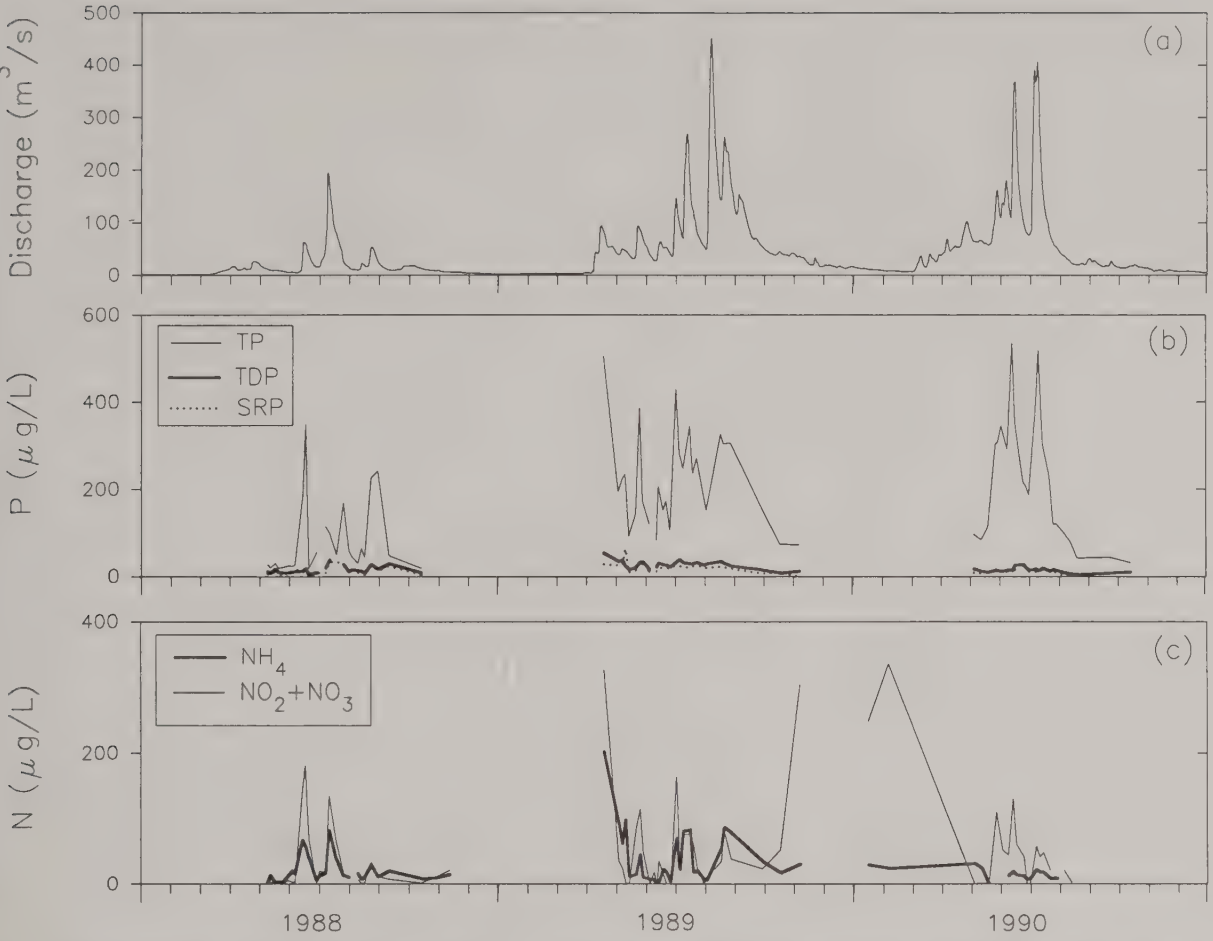

FIG. 2. Surface-water data for the Pembina River, Alberta: (a) discharge rate 83 km upstream of the mouth (Environment Canada 1989, 1990, and 1991) and (b) phosphorus (TP, TDP, and SRP) and (c) nitrogen (NO_2 + NO_3 and NH_4) concentrations averaged for sites located 27, 83, and 152 km upstream of the mouth.

ences in open-water, porewater, or sediment chemistry between sites, dates, or depth strata. Regression analysis was used to relate porewater and sediment phosphorus and nitrogen concentrations to open-water SRP and NH_4, instantaneous current velocity, and discharge rate (integrated over the sampling date or averaged over the 2-wk period prior to sampling) for each depth stratum, with site (fine sediment, cobble, or sand) introduced as a dummy variable in the regression. Results are presented as mean ± SE in the text; mean values are plotted in the figures.

Results

Surface Water

Discharge varied considerably both within and between years (Fig. 2a). Flows peaked at 193, 451, and 406 m^3/s in 1988, 1989 and 1990, respectively. Minimum flows occurred in winter (January and February) with values of 1, 3, and 8 m^3/s recorded for 1988, 1989, and 1990, respectively. Discharge rates for the May–November study period averaged 22, 87, and 68 m^3/s for 1988, 1989, and 1990, respectively; the 30-yr (1958–88) average for this time period is 45 m^3/s (Environment Canada 1988). Subsurface current speed was correlated with discharge rate for the sand site ($r = 0.61$, $P < 0.001$) and averaged 0.75 ± 0.04, 0.44 ± 0.02, and 0.28 ± 0.03 m/s for the cobble, sand and fine-sediment sites, respectively, for May–November 1989–90.

Open-water SRP, TP, and inorganic nitrogen (NO_2 + NO_3 and NH_4) concentrations were not significantly different ($P > 0.06$; MANOVA, SNK) among the three sites. TDP concentrations were, however, slightly greater ($0.01 < P < 0.05$; SNK test) at the fine-sediment site than at the cobble site; concentrations at the sand site were intermediate to and not significantly different ($P > 0.1$; SNK test) from the other two sites. Overall, open-water nutrient concentrations averaged 169, 19.6, and 14.6 μg TP, TDP, and SRP/L, respectively, and 49.1 and 28.5 μg NO_2 + NO_3 and NH_4/L, respectively, for the entire study (Fig. 2b and 2c). Temporal variations in open-water phosphorus concentrations were associated with changes in discharge rate, largely as a result of an increase in the particulate load. Daily measurements of open-water TP at the fine-sediment site for June–October 1988 and May–July 1989 were significantly correlated with discharge rate ($P < 0.0001$, $r = 0.38$, $n = 170$).

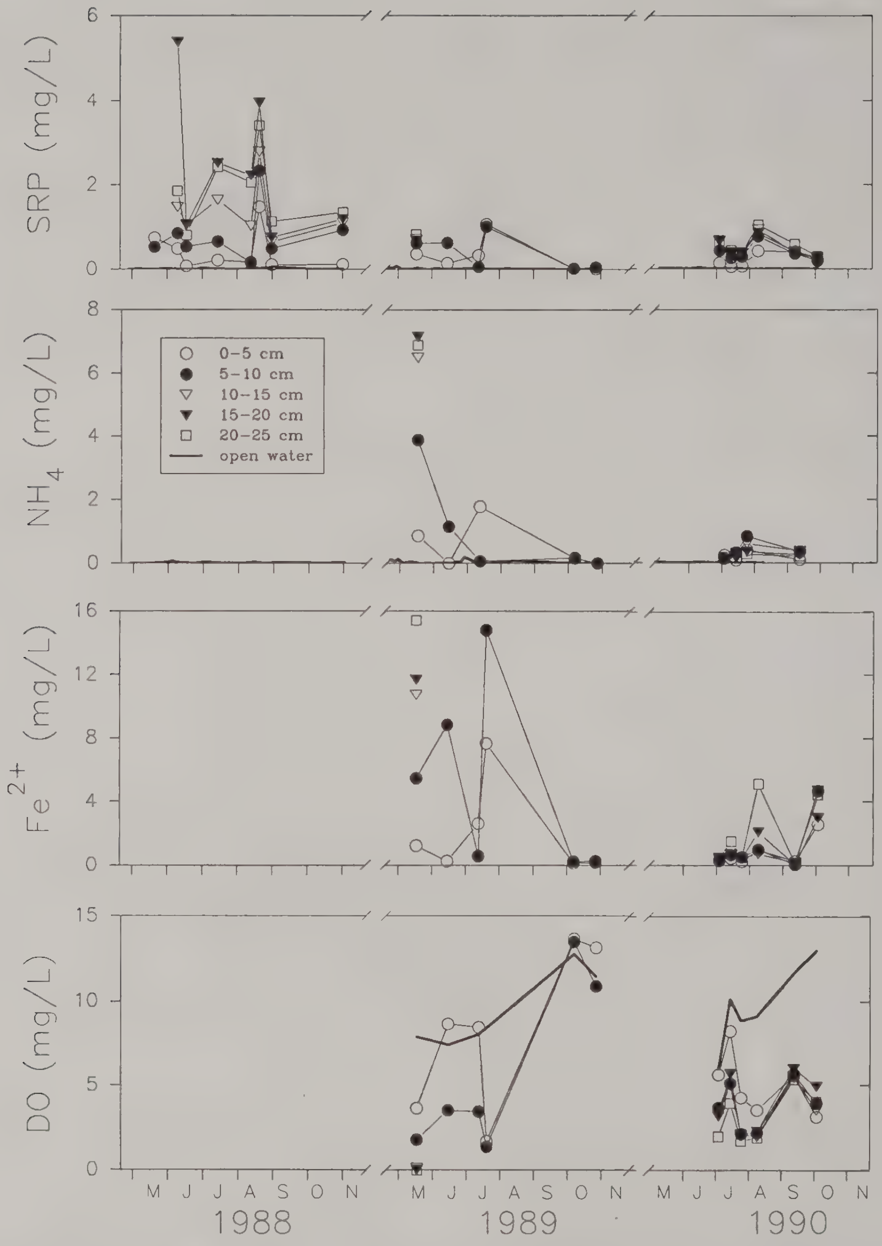

FIG. 3. Open-water SRP, NH_4, and DO concentrations and porewater SRP, NH_4, Fe^{2+}, and DO concentrations at five depth intervals into the riverbed for the fine-sediment site on the Pembina River, Alberta. (Open-water concentrations are not always distinguishable from zero on these scales. Note changes in scale for SRP, NH_4, and Fe^{2+} between Fig. 3, 4, and 5.)

Porewater Chemistry

In contrast with the open-water chemistry, porewater nutrient concentrations differed significantly ($P < 0.0001$, $F > 12$; MANOVA) between sites (Fig. 3, 4, and 5). Porewater values for 1989 and 1990 for all depths averaged 70 ± 11, 210 ± 23, and 438 ± 33 μg SRP/L and 97 ± 9, 232 ± 26, and 1407 ± 293 μg NH_4/L for the sand, cobble, and fine-sediment sites, respectively. Fe^{2+} concentrations were also greater for the fine-sediment site (2.9 ± 0.5 mg/L) than for the cobble (1.1 ± 0.2 mg/L) or sand (0.4 ± 0.07 mg/L) site, while DO concentrations decreased from 6.4 ± 0.2 to 5.8 ± 0.4 to 4.3 ± 0.4 mg/L for the sand, cobble, and fine-sediment sites, respectively. Ca^{2+} data are only available for two or three dates in each of 1989 and 1990 and averaged 56 ± 4, 79 ± 9, and 50 ± 6 mg/L for the three sites, respectively.

In addition to variation between sites, porewater composition also varied with depth and over time. At the fine-sediment site, porewater SRP concentrations in the 0–5 cm depth stratum varied as much as 400-fold within a single year (Fig. 3). This variation was consistent with depth such that porewater SRP

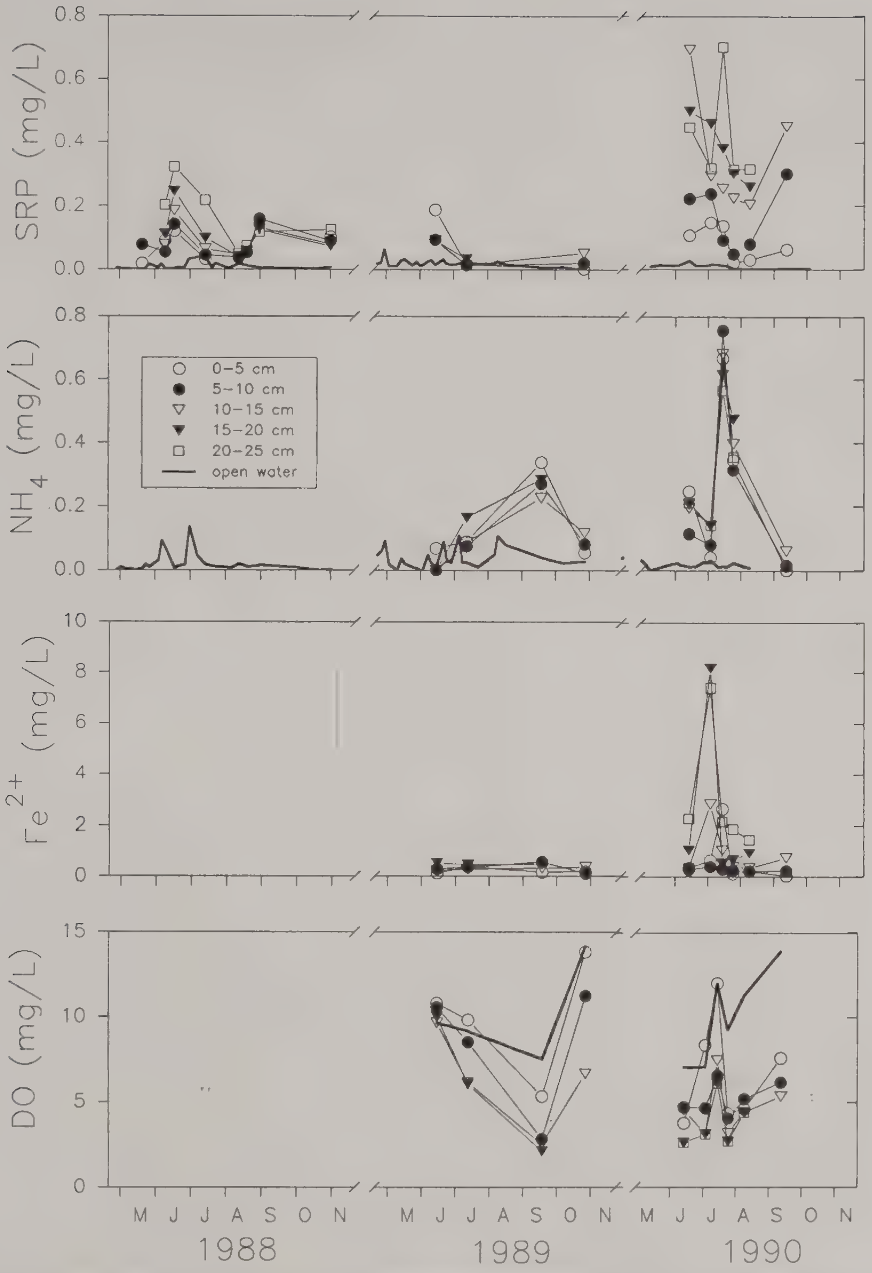

FIG. 4. Open-water SRP, NH_4, and DO concentrations and porewater SRP, NH_4, Fe^{2+}, and DO concentrations at five depth intervals into the riverbed for the cobble site on the Pembina River, Alberta. (Note changes in scale for SRP, NH_4, and Fe^{2+} between Fig. 3, 4, and 5.)

concentrations increased with depth and all depth strata varied in synchrony; there was no interaction between date and depth ($P > 0.5$, $F = 1.0$; ANOVA). Porewater NH_4, Fe^{2+}, and DO data are only available for 1989 and 1990. During these years, NH_4, Fe^{2+}, and DO concentrations also varied with date ($P < 0.0001$, $F > 10$; MANOVA) and depth ($P < 0.05$, $F > 2.6$; MANOVA). However, depth profiles of these compounds were less uniform, with the depth of maximum concentration varying between dates. Porewater SRP and NH_4 concentrations were consistently greater than open-water values with the exception of mid-June to mid-July 1989 when porewater NH_4 concentrations approximated open-water values. While open-water DO concentrations generally exceeded porewater values in 1990, there was no consistent relationship between DO in the porewater and open-water pools in 1989.

Porewater SRP concentrations at the cobble site also varied considerably over the 6-mo sampling period, even for the deepest strata (Fig. 4). However, unlike the fine-sediment site, there was an interaction between date and depth ($P < 0.001$, $F = 2.53$; ANOVA) such that the depth of maximum SRP con-

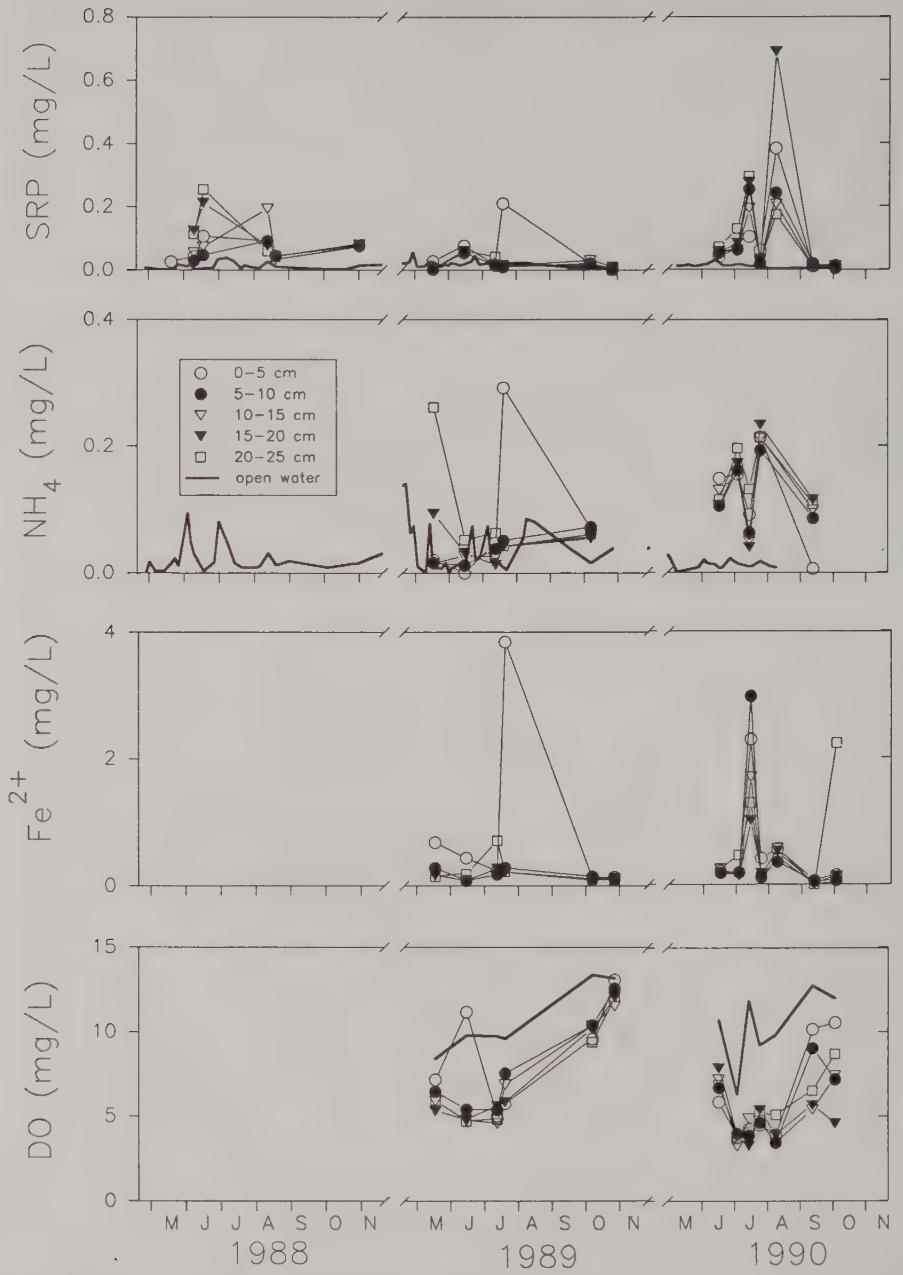

FIG. 5. Open-water SRP, NH_4, and DO concentrations and porewater SRP, NH_4, Fe^{2+}, and DO concentrations at five depth intervals into the riverbed for the sand site on the Pembina River, Alberta. (Note changes in scale for SRP, NH_4, and Fe^{2+} between Fig. 3, 4, and 5.)

centration varied over time. NH_4, Fe^{2+}, and DO concentrations also varied with date ($P < 0.0001$, $F > 6.4$; MANOVA); however, NH_4 concentrations showed only weak depth stratification ($P = 0.06$, $F = 2.5$; MANOVA), while depth gradients were established for DO and Fe^{2+}. Porewater SRP and NH_4 concentrations were greater than open-water values with the exception of several months in 1989 when porewater values approximated open-water concentrations. DO concentrations were similar for both open water and pore water in June 1989; thereafter, open-water DO concentrations were similar to porewater values for the 0–5 cm depth stratum but greater than values for deeper strata.

Porewater SRP, NH_4, DO, and Fe^{2+} concentrations at the sand site also varied considerably over time; however, unlike both the cobble and fine-sediment sites, porewater SRP concentrations at the sand site showed little if any depth stratification ($P > 0.07$, $F = 2.22$; ANOVA) (Fig. 5). Porewater NH_4 and Fe^{2+} concentrations were also poorly stratified; however, DO concentrations increased with depth ($P < 0.01$, $F = 5.0$; MANOVA). Despite the absence of well-defined

TABLE 1. Correlation matrix for porewater SRP, NH_4, Fe^{2+}, DO, and Ca^{2+} concentrations for all depth strata and all sites on the Pembina River, Alberta. Data presented as Pearson correlation coefficients (r) and sample size. $^*0.01 < P < 0.05$; $^{***}P < 0.0001$.

	SRP	NH_4	Fe^{2+}	DO	Ca^{2+}
SRP	1.00 (474)				
NH_4	0.57^{***} (227)	1.00 (235)			
Fe^{2+}	0.58^{***} (296)	0.82^{***} (235)	1.00 (304)		
DO	-0.56^{***} (293)	-0.40^{***} (232)	-0.39^{***} (301)	1.00 (301)	
Ca^{2+}	0.20^{*} (125)	0.20^{*} (121)	0.23^{*} (125)	-0.42^{***} (123)	1.00 (125)

depth gradients, porewater SRP and NH_4 concentrations were consistently greater than open-water values for 1988 and 1990. In 1989, porewater and open-water SRP and NH_4 concentrations were similar. Open-water DO concentrations usually exceeded porewater values.

Porewater SRP, NH_4, Fe^{2+}, DO, and Ca^{2+} concentrations were highly intercorrelated (Table 1). Analysis of porewater data for all sites and depths showed that SRP, NH_4, Fe^{2+}, and Ca^{2+} concentrations were all positively correlated with one another and negatively correlated with DO.

Sediment Chemistry

Sediment nutrient concentrations differed significantly between sites ($P < 0.0001$, $F > 68$; MANOVA). Exchangeable phosphorus concentrations for 1989 and 1990 for all depth strata averaged 280 ± 12 μg/g for the fine-sediment site compared with 256 ± 14 and 83 ± 5 μg/g for the cobble and sand sites, respectively (Fig. 6). In contrast with the porewater SRP data, exchangeable phosphorus concentrations were usually less variable over time. Annual variability (calculated as the difference between concentrations for individual dates and the annual mean value, expressed as a percentage of the annual mean) for the 0–5 cm depth stratum averaged less than 20% for the fine-sediment site and between 22 and 40% for the cobble site. By comparison, porewater SRP concentrations varied, on average, by 64–85% for the fine-sediment site and by 52–115% for the cobble site. Phosphorus concentrations at the sand site were highly variable for both the sediment-exchangeable (22–88% of the annual mean) and porewater (40–95% of the annual mean) pools. Depth profiles are only available for seven dates for the cobble and fine-sediment sites and 14 dates for the sand site. On these dates, exchangeable phosphorus concentrations tended to increase with depth at the cobble and sand sites ($P < 0.001$, $F > 5.7$; ANOVA) but showed no significant difference with depth for the fine-sediment site ($P > 0.4$, $F = 0.76$; ANOVA).

Exchangeable nitrogen concentrations also differed between sites, averaging 25 ± 4, 1.7 ± 0.2, and 1.2 ± 0.1 μg/g for the fine-sediment, cobble, and sand sites, respectively (1989–90 data for all depth strata) (Fig. 7). Nitrogen concentrations showed less temporal variability in the sediment than in the porewater pool, with annual variation in the sediment pool averaging 53–57% for the fine-sediment and cobble sites compared with values of 75–85% for the porewater pool. At the sand site, nitrogen concentrations varied by 73% of the annual mean for both the porewater and sediment pools. There was at best weak stratification ($0.01 < P < 0.08$) of exchangeable nitrogen with depth into the sediments for all sites.

Riverbed Chemistry in Relation to Flow

Comparison of mean annual phosphorus concentrations for the porewater pool showed that for all three sites, phosphorus concentrations were depressed in 1989, the high-flow year, relative to the low-flow conditions of 1988 (Fig. 8). The return to intermediate flows in 1990 coincided with an increase in phosphorus concentrations in the porewater at both the cobble and sand sites. While NH_4, Fe^{2+}, Ca^{2+}, and DO data are available only for 1989 and 1990, changes in concentration of these elements were consistent with those of the phosphorus pool, with lower NH_4, Fe^{2+}, and Ca^{2+} and higher DO concentrations in 1989 than in 1990 for both the cobble and sand sites. In contrast, riverbed chemistry at the fine-sediment site did not respond to the reduction in flow from 1989 to 1990: porewater SRP concentrations were unchanged, while Fe^{2+}, NH_4, and Ca^{2+} decreased between 1989 and 1990. These interannual changes in porewater chemistry appeared to be correlated with changes in the particle size composition of the riverbed. At the sand site, the bottom sediments were initially composed almost entirely of sand which changed to a mixture of sand, silt, and clay after the high-flow conditions of 1989 and then reverted back to a predominately sand substrate by midsummer 1990 (Fig. 9). Sediments at the cobble site were dominated by sand throughout the study although the proportion of sand decreased and clay increased throughout 1988 and 1990. At the fine-sediment site, the initial silt/clay sediments were replaced by a primarily sand substrate after the 1989 storms and sand continued to dominate the sediment profile for the remainder of 1990.

While interannual variation in porewater and sediment nutrient concentrations was related to changes in discharge, temporal changes on a shorter time scale were not correlated with flow. Porewater SRP and NH_4 concentrations were not related ($P > 0.1$) to instantaneous current velocity or discharge rate (integrated over the sampling date or averaged over the 2 wk prior to sampling) for any of the five depth strata. Likewise, sediment-exchangeable nutrient concentrations were not correlated ($P > 0.1$) with current velocity or discharge rate with the exception of a positive relationship ($P < 0.05$) between exchangeable phosphorus and current velocity or instantaneous discharge for the 0–5 and 5–10 cm depth strata. Changes in porewater SRP or NH_4 concentrations showed no correlation ($P > 0.2$) with open-water nutrient concentrations. There was also no relationship ($r < 0.39$, $P > 0.06$) between sediment-exchangeable and porewater phosphorus or nitrogen.

Discussion

Nutrient concentrations in the bottom sediments of the Pembina River varied between sites, over time, and with depth. Overall, porewater values ranged from below detection limits to maxima of 5.4, 7.2, and 15.4 mg SRP, NH_4, and Fe^{2+}/L, respectively. While few data exist on porewater chemistry of rivers, the concentrations we recorded are greater than values previously reported for small streams (Dahm et al. 1987) and approach or exceed the maxima recorded for many eutrophic and hypereutrophic lakes (Enell and Lofgren 1988; Shaw and Prepas 1990). Porewater nutrient concentrations were negatively correlated with DO such that the highest SRP, NH_4, and Fe^{2+} values were recorded when DO concentrations were relatively low (<2 to 4 mg/L). DO concentrations, however, rarely approached 0 mg/L. These unusually high NH_4 and Fe^{2+} con-

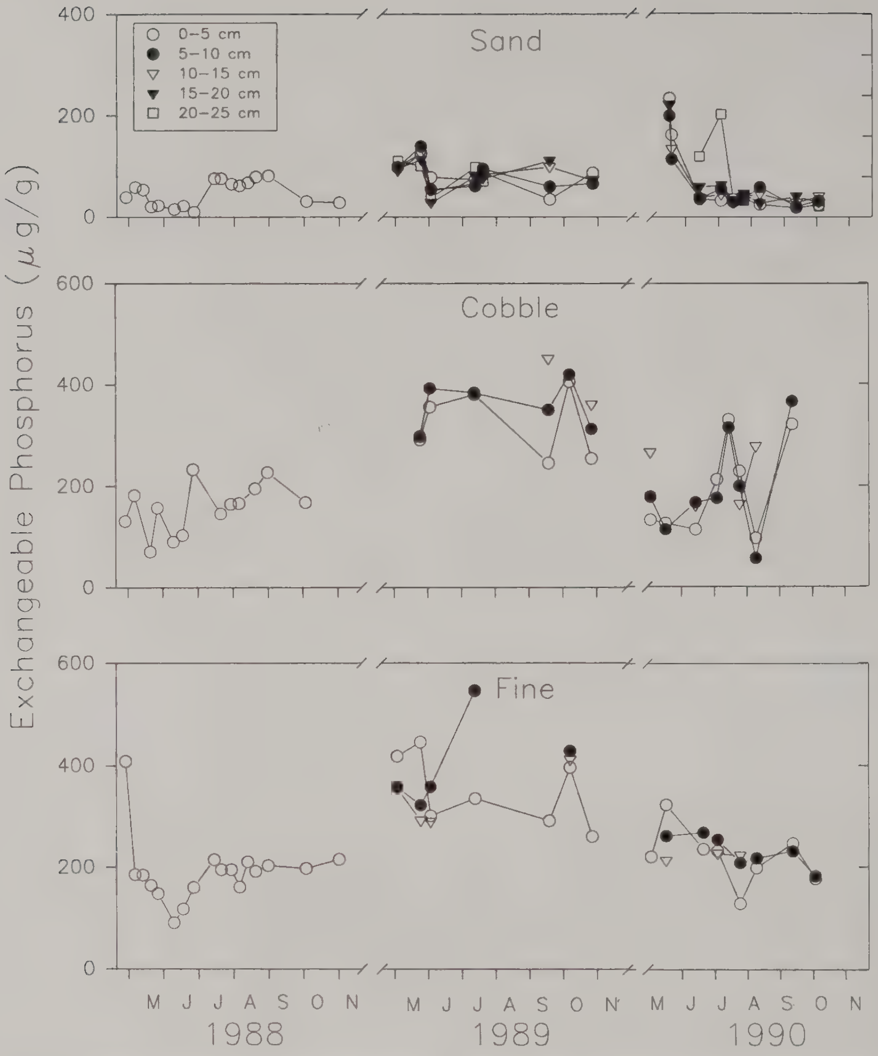

FIG. 6. Exchangeable phosphorus concentrations at five depth intervals into the riverbed for three sites on the Pembina River, Alberta.

centrations in the presence of oxygen may be attributable to the fact that we pooled porewater samples that may have differed in DO content. Differences in DO and nutrient concentrations were observed between samples collected from replicate samplers placed side-by-side in the riverbed and resulted in average SRP, NH_4, and Fe^{2+} concentrations that were greater than would be expected on the basis of the average DO content (e.g. Fig. 3: May 1989 for the 0–5 and 5–10 cm depth strata). In addition to horizontal patchiness, riverbed sediments may be stratified vertically over smaller intervals than the 5-cm strata that we pooled. Thus, our sampling programme may have integrated waters containing a range of oxygen and nutrient concentrations. Despite this spatial heterogeneity in riverbed chemistry, porewater nutrient concentrations varied consistently such that SRP, NH_4, and Fe^{2+} were greater at lower DO concentrations.

Differences in nutrient concentrations between sites and depth strata were correlated with riverbed composition. Thus, porewater SRP, NH_4, and Fe^{2+} concentrations increased, while DO concentrations decreased as sediment particle size decreased from the sand through to the cobble and fine-sediment sites. Strong depth gradients were also established at the fine-sediment site whereby porewater SRP concentrations increased and NH_4, Fe^{2+}, and DO concentrations varied with depth into the riverbed. In contrast with the fine-sediment site, porewater gradients at the cobble and sand sites were either never established or less consistent with depth. Variations in porewater nutrient concentrations as a function of substrate composition have been clearly documented for both lakes (Frevert 1979) and streams (Dahm et al. 1987; White et al. 1987; Triska et al. 1989) and are attributable to differences in sorption capacity, mineralization and decomposition rates, permeability, oxygen availability, microbial activity, and groundwater intrusion (Syers et al. 1973). However, while gradients in nutrient concentrations across the sediment–water interface and into the deeper sediments are typical of lakes, their occurrence in flowing waters is less predictable. Tracer studies on a small Appalachian stream have shown that the porewater pool (down to depths of 10 cm) reached equilibrium with the surface waters within 25 min for both coarse (64–256 μm) and fine (<2 μm) sediments (Munn and Meyer 1988). Likewise, DO concentrations in a small mountain stream were similar for surface water

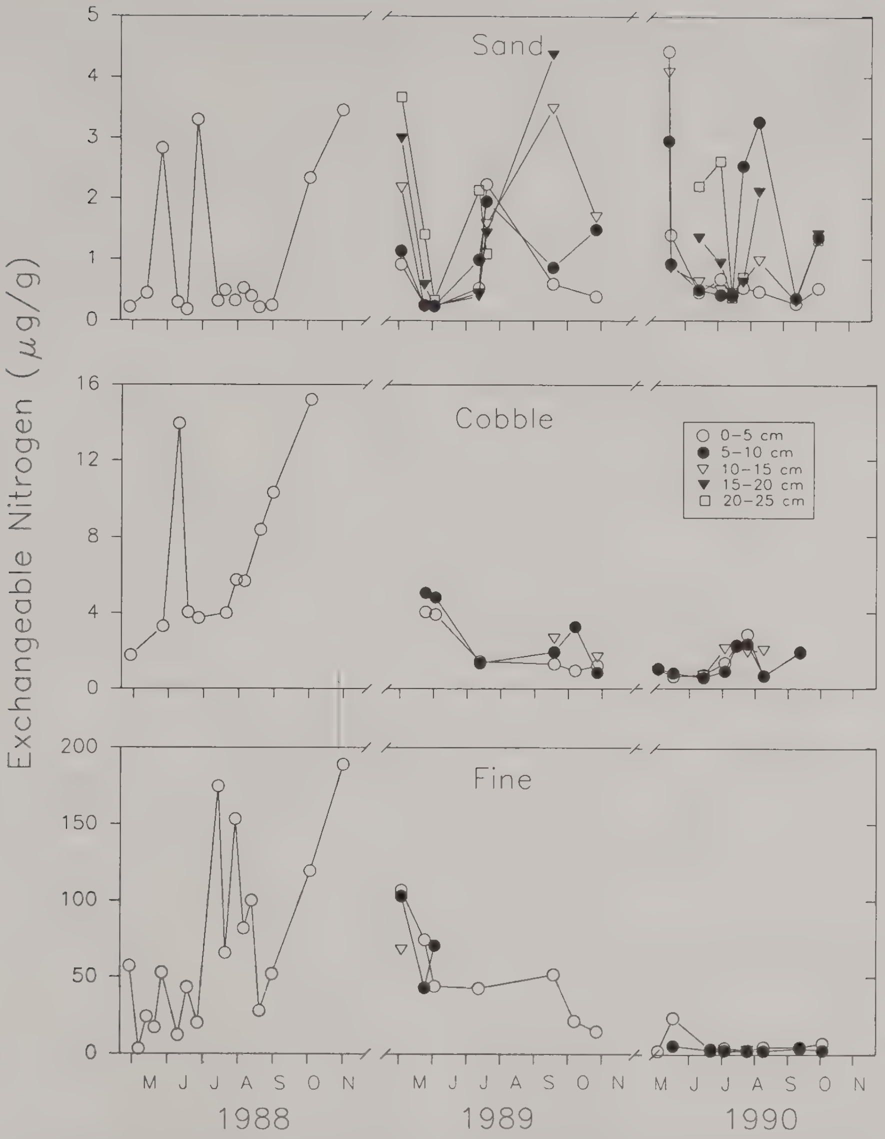

FIG. 7. Exchangeable nitrogen concentrations at five depth intervals into the riverbed for three sites on the Pembina River, Alberta. (Note changes in scale for the three sites.)

samples and hyporheic samples collected at distances up to 4 m from the channel (Triska et al. 1990), while in other streams, 85–100% oxygen saturation has been reported at depths of 0.2–1 m below the sediment-water interface (Woods 1980; Bretschko 1981). In contrast, DO concentrations in some streams have been reported to decrease from near saturation in the surface waters to near anoxia at 5 cm into the riverbed, even for relatively coarse (>125 μm) sediments (Dahm et al. 1987; Strommer and Smock 1989). In the Pembina River, the presence of nutrient and DO gradients across the sediment–water interface and into the deeper sediments was correlated with sediment particle size such that gradients were stronger and less easily disrupted by flow in fine than in coarse or sand substrates. In other locales, however, sediment permeability may not be related to the degree of similarity between surface water and porewater because changes in channel morphology (Vaux 1962, 1968; Savant et al. 1987; Thibodeaux and Boyle 1987) and groundwater upwelling (see Wetzel and Manny 1977; Sowden and Power 1985; Ford and Naiman 1989; Pringle and Triska 1991) may disrupt sediment–water gradients.

In addition to variations in riverbed chemistry between sites and depth, porewater SRP, NH_4, Fe^{2+} and DO concentrations also varied over time. In the case of SRP, concentrations in the pore water varied by as much as 400-fold within a single year, with annual variability averaging 40–115% of annual mean values. Similarly, NH_4 concentrations varied by as much as 3 orders of magnitude within a single year, averaging 49–111% of mean values. Few studies have examined temporal dynamics in riverbed porewater chemistry and among those that have, the emphasis has been on small, low-discharge streams (<0.1 m^3/s mean annual discharge). In these systems, DO concentrations were lower and the number of anoxic samples greater

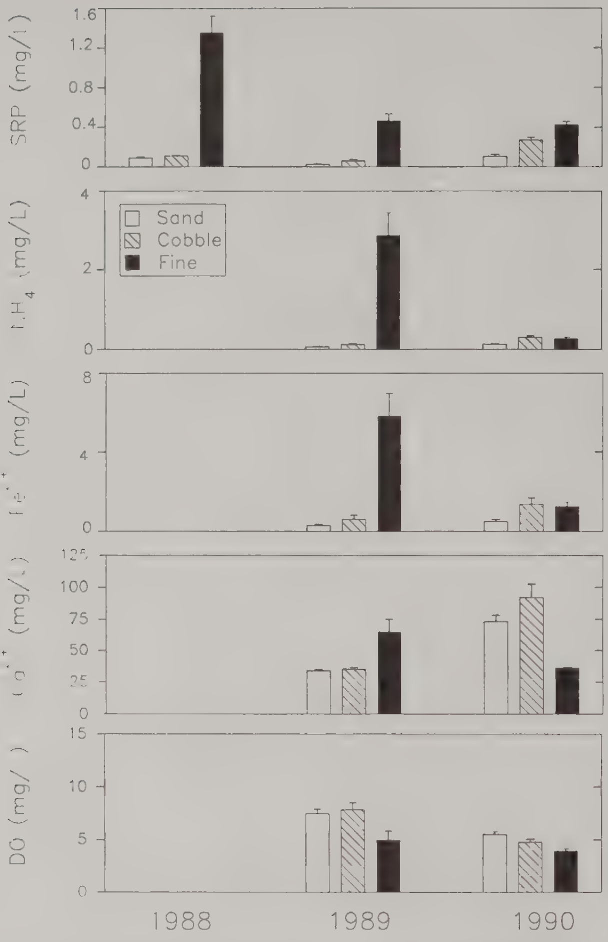

FIG. 8. Mean annual concentrations (±SE) of porewater SRP, NH_4, Fe^{2+}, Ca^{2+}, and DO in the Pembina River, Alberta, at three sites differing in riverbed composition.

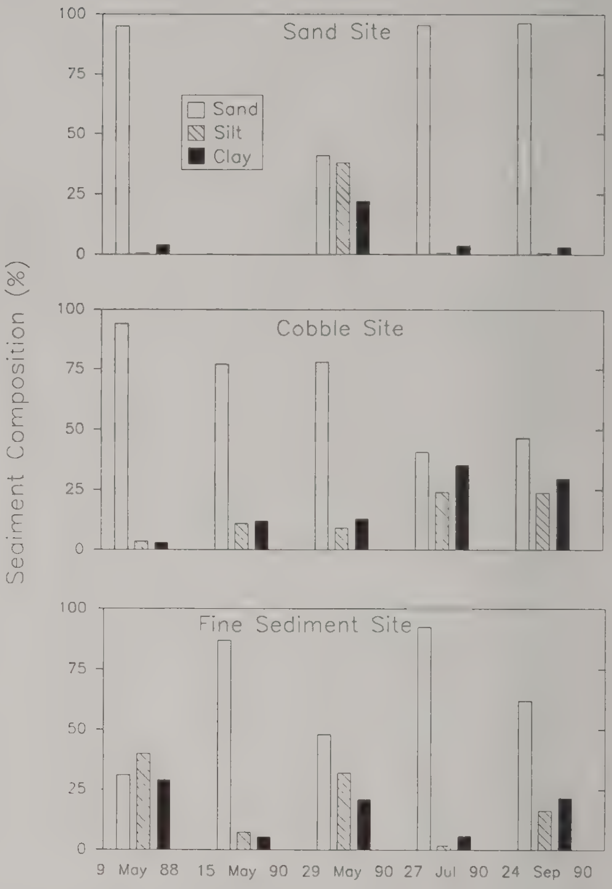

FIG. 9. Particle size of riverbed sediments collected from 0–5 cm below the sediment–water interface for three sites on the Pembina River, Alberta. (Data are not available for the sand site on 15 May 1990.)

during summer than in winter (Whitman and Clark 1982; Carr 1989; Strommer and Smock 1989). Seasonal patterns in NH_4 dynamics have also been observed whereby concentrations increased during summer (Carr 1989). The observation that in small streams, intraannual variability in porewater chemistry tracks seasonal patterns is consistent with studies of porewater dynamics in lakes: interstitial SRP and NH_4 concentrations tend to increase in late summer and are minimal during winter (Carignan 1985; Enell and Lofgren 1988). However, in contrast with lentic and slow-flowing systems, there was no apparent seasonal pattern in porewater chemistry in the higher discharge (45 m^3/s annual mean, 1958–88) Pembina River. The time of peak concentration and the depth strata in which it occurred varied between years as well as between sites. Moreover, these temporal changes in porewater chemistry were not correlated with changes in either surface-water or sediment nutrient concentrations. By comparison, porewater and surface-water nutrient concentrations were strongly correlated ($P < 0.01$) for three slow-flowing streams (after Carr 1989) and nine Alberta lakes (Shaw and Prepas 1990), suggesting that nutrients were exchanged between surface and porewater pools. Our observation that porewater SRP and NH_4 concentrations for the Pembina River were, with the exception of several months during high-flow conditions, greater than surface water values indicates the potential for nutrient release from the riverbed to the overlying water. However, our finding that open-water and porewater nutrient concentrations were not correlated and that open-water SRP concentrations did not differ between sites with different bottom substrates indicates that the riverbed had little measurable impact on open-water nutrient concentrations. By comparison, riverbed sediments have been implicated as a buffer system in the control of surface-water SRP concentrations for small streams (Taylor and Kunishi 1971; Meyer 1979; Klotz 1988) and the low-nutrient (<10 μg SRP/L) waters of the Amazon River (Gessner 1960).

Comparison of porewater chemistry between years showed that interannual variation in riverbed chemistry was related to discharge and corresponding changes in the size composition of the bottom sediments. For the cobble and sand sites, porewater SRP concentrations were higher during low-discharge regimes (1988) than during high flows (1989); concentrations were greatest under the intermediate regime of 1990 (Fig. 8). At the fine-sediment site, however, the reduction in porewater SRP concentrations from 1988 to 1989 in response to higher flows was not followed by a return to higher concentrations during the intermediate flows of 1990. Rather, porewater SRP and DO concentrations remained unchanged, while porewater Fe^{2+} and NH_4 concentrations decreased between 1989 and 1990. Comparison of riverbed composition before (May 1988) and after (1990) the high flows showed that for the sand and cobble sites, there had been a temporary (sand site) or longer-term (cobble site) increase in the proportion of fine material (Fig. 9). At the fine-sediment site, however, the proportion of sand had increased from 31% in May 1988 to between 48 and 87% in 1990. The decrease in silts and clays at the fine-sediment site and their increase at the two downstream sites indicate that the high-discharge event in the summer of 1989 caused bedload transport with fine material being picked up and transported to sites downstream. In contrast, the intermediate-discharge regime of summer 1990 caused silts and clays to be mobilized from the sand site but not the cobble site where fine sediments tended to accumulate between cobble crevices. These changes in riverbed composition after the high flows of 1989 were consistent with the changes we observed in porewater chemistry, namely, that lower porewater nutrient concentrations were associated with coarser sediments. However, while changes in porewater chemistry between years were related to flow and riverbed composition, intraannual changes were rarely correlated with changes in instantaneous velocity or with discharge rate. Triska et al. (1989) and H.-H. Schmidt (pers. comm.) indicated that for small headwater streams, intraannual changes in porewater and hyporheic chemistry were related to flow. Our results suggest that in larger unregulated rivers, large-scale changes in discharge act as set-points in defining the composition and chemistry of the bottom sediments. The effect of day-to-day changes in water flow on riverbed chemistry in these systems appears minimal and likely masked by other factors such as time-lag responses to changes in flow and changes in the binding efficiency of the sediments. Tessenow (1974) showed that in oxic water, iron was less efficient at binding phosphorus when Fe/P molar ratios were less than 1.8. Comparison of porewater Fe/P molar ratios for the 9–13 sampling dates for which data are available showed that ratios were less than 1.8 for two or more depth strata on five, five, and three dates for the fine, cobble, and sand sites, respectively. This suggests that the binding efficiency of the sediments for phosphorus, and possibly other ions, varied over the year. While variable inputs from groundwater may also cause temporal changes in porewater chemistry, riverbed chemistry in the South Saskatchewan River downstream of Saskatoon, Saskatchewan, was just as variable as that in the Pembina River even though measurements of deuterium levels in porewater samples collected 0–30 cm into the South Saskatchewan riverbed gave no evidence of groundwater intrusion (R. J. Cornett and P. A. Chambers, unpubl. data).

In summary, our results showed that riverbed chemistry is highly dynamic, with dramatic shifts in SRP, NH_4, Fe^{2+}, and DO concentrations occurring even in fine depositional sediments at depths of 20–25 cm below the sediment–water interface. Interannual changes in riverbed chemistry were related to flow such that high flows (twice the long-term average) were associated with decreased nutrient and increased DO concentrations in the pore water, irrespective of the nature of the riverbed. These large-scale changes in flow acted as a set-point mechanism and changed both the particle size composition and porewater chemistry of the riverbed. On a shorter time scale, however, variations in riverbed chemistry between May and November could not be predicted from flow, current velocity, or open-water chemistry, likely because of the confounding effects of time-lag responses to changes in flow and changes in the binding efficiency of the sediments. The highly dynamic nature of riverbed chemistry has important implications for benthic productivity as well as for the transfer of material between surface waters and the riverbed. First, benthic organisms inhabit an environment characterized by dynamic and often unpredictable changes in DO and nutrient concentrations. Second, dramatic changes in the chemistry of the riverbed can occur in the span of a year, even without a flushing scour, which may result in the transport of compounds through the riverbed and across the sediment–water interface.

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Aquatic Insects as Bioindicators of Trace Element Contamination in Cobble-Bottom Rivers and Streams

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Trace element bioaccumulation was studied in immature benthic insects from two contaminated river systems to develop these animals as bioindicators. In one river, Cu, Cd, Pb, and Zn were analysed in insects and in fine bed sediments over a 381-km reach downstream of a large copper mining complex. In the other river, As contamination from a gold mine was assessed in insects and bed sediments over a 40-km reach. All insect taxa collected in contaminated river reaches had elevated whole-body trace element concentrations. However, direct comparisons of contamination using a single, common species among stations were limited because few species were distributed throughout the study reaches. Comparisons of contamination at taxomic levels higher than species were complicated by element-specific differences in bioaccumulation among taxa. These differences appeared to be governed by biological and hydrogeochemical factors. The variation in element concentrations among species of the caddisfly *Hydropsyche* was slightly greater than within individual species. If this genus is representative of others, comparisons of contamination within genera may be a practical alternative for biomonitoring studies when single species are not available.

On a étudié la bioaccumulation d'éléments traces chez des insectes benthiques immatures dans deux réseaux de cours d'eau pollués pour utiliser ces animaux comme bioindicateurs. Dans une rivière, on a mesuré Cu, Cd, Pb et Zn chez les insectes et dans les sédiments fins du lit sur un tronçon de 381 km en aval d'un grand complexe d'extraction du cuivre. Dans l'autre cours d'eau, on a mesuré la contamination par l'As provenant d'une mine d'or chez les insectes et dans les sédiments du lit sur un tronçon de 40 km. Tous les taxons d'insectes prélevés dans les tronçons pollués présentaient des concentrations élevées d'éléments traces à l'échelle corporelle. Toutefois, les comparaisons directes de la pollution sur une seule espèce commune aux diverses stations étaient limitées du fait qu'on retrouvait peu d'espèces disséminées tout au long des tronçons de l'étude. La comparaison de la pollution à des niveaux taxinomiques supérieurs à l'espèce était rendue difficile par des différences dans la bioaccumulation selon les éléments parmi les taxons. Ces différences semblaient régles par des facteurs biologiques et hydrogéochimiques. La variation des concentrations en éléments entre les espèces de la phrygane *Hydropsyche* était légèrement supérieure à celle qu'on observait au sein de chaque espèce. Si ce genre était représentatif des autres, la comparaison de la pollution entre les genres pourrait être une solution intéressante dans les études de surveillance biologique lorsqu'on ne peut étudier une espèce donnée.

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The extraction and processing of metal-rich ores in watersheds can result in extensive trace element contamination of streams and rivers by the downstream transport of waste material (Andrews 1987; Goddard 1988; Moore and Luoma 1990; Axtmann and Luoma 1991). Bioaccumulation data can be used to assess the occurrence and biological significance of such contaminants (Burrows and Whitton 1983; Hatakeyama et al. 1988; Lynch et al. 1988; Axtmann et al. 1991; Moore et al. 1991). The insect community is one of the most important faunal components in cobble-bottom streams, and immature benthic insects satisfy several important criteria established for biological indicators (Phillips 1980). Insects accumulate excessive amounts of trace elements when exposed to unnaturally high concentrations (Nehring 1976; Spehar et al. 1978; Burrows and Whitton 1983; Besser and Rabeni 1987). Some taxa tolerate high body burdens of trace elements (Burrows and Whitton 1983; Hatakeyama et al. 1988). Many taxa are sedentary; thus, body burdens reflect local conditions, although contaminant concentrations in taxa that tend to drift may also reflect conditions at upstream sites that were previously occupied (Gower and Darlington 1990). Time-integrated measurements of exposure can be made with species whose immature aquatic life history extends for months or years. Lastly, benthic insects can be collected by simple, inexpensive methods.

There are, however, important, unresolved problems in using aquatic insects as bioindicators. Few studies have reported how bioaccumulation of trace elements is related to concentrations in the environment. The small size of most insects often requires many individuals to be pooled to ensure that each sample has sufficient biomass to meet analytical detection limits for trace elements. This method sacrifices information on individual variation. Also, in bioindicator studies, there is an implicit understanding that direct comparisons of contamination can only be made within species because of species-specific differences in contaminant uptake. However, populations of stream-dwelling insects vary considerably with time and location, and direct comparisons of contamination among locations may be limited by the absence of a single, common species. An alternative to studying a common species might be to group data from different taxa, e.g. genus, family, and order. This approach would allow comparisons of contamination among more locations, but the effect of such pooling on the reliability of those comparisons has not been rigorously determined.

This paper considers three questions pertinent to using benthic insects as bioindicators of trace element contamination in rivers and streams: (1) which taxa are available for assessments of contamination over large spatial scales, (2) do chemical data from a suite of different taxa provide a body of evidence which reliably describes contamination gradients, and (3) in lieu of a single species, can strategies be developed for grouping taxa without a critical loss in sensitivity to changes in contaminant exposure?

The above questions are addressed with data from two separate, contaminated river systems in the United States. Spatial distributions of individual species and genera were examined in each river. The biological responses to contamination in these taxa were assessed by comparing bioaccumulation with contaminant concentrations in fine bed sediments. The influences of taxonomic relationship, feeding habit (Smock 1983a), and insect size (Smock 1983b; Krantzberg and Stokes 1988; Cain et al. 1989) on interspecies differences in bioaccumulation were examined.

Materials and Methods

Site Descriptions

The Clark Fork River in Montana and Whitewood Creek in South Dakota are similar in physical characteristics and origin of contamination. Both river systems have cobble–boulder and gravel–rubble substrata and have been extensively contaminated by large-scale mining in or near their headwaters. The river systems differ with respect to the primary contaminants and geochemical conditions affecting the chemical form and distribution of the contaminants and in the species composition of the benthic community, thus broadening the scope of our analysis of benthic insects as bioindicators.

A large copper mining and smelting complex was established in the headwaters of the Clark Fork River system in the 1860's. Mining declined in the 1970's, but between 1864 and 1972, more than 10^8 t of waste material enriched with heavy metals (e.g. Cu, Fe, Pb, Cd, and Zn) was released via Silver Bow Creek and Warm Springs Creek to the river (Fig. 1) and deposited in floodplains and bed sediments (Andrews 1987; Moore and Luoma 1990; Axtmann and Luoma 1991). Acid mine drainage is not common in this system. Nevertheless, contaminated bed sediments extend at least 550 km below the original site of mining activities (Johns and Moore 1985; Rice and Ray 1985; Brook and Moore 1988; Moore and Luoma 1990; Axtmann and Luoma 1991), presumably as a result of the transport of contaminated particulate materials. Trace metal contamination in benthic invertebrates has been detected 381 km downriver (Moore and Luoma 1990; Axtmann et al. 1991).

Whitewood Creek has been heavily contaminated by the discharge of tailings from a large gold mine located in the city of Lead (Fig. 2). From 1876 to 1977, mine tailings were discharged via a small tributary, Gold Run, into Whitewood Creek (Goddard 1988). The primary contaminant in Whitewood Creek is As which is derived from arsenopyrite, a common mineral in the gold-bearing deposits (Goddard 1988). Transport and deposition of the discharged tailings led to extensive downstream As contamination of bed and floodplain sediments and biota in Whitewood Creek and the Belle Fourche River (Cherry et al. 1986; Cain et al. 1989; Marron 1989; McKallip et al. 1989; Kuwabara et al. 1990). An important aspect of the As contamination is remobilization of As and ferrous iron in acidic groundwater which flows from contaminated alluvial deposits into the creek (Fuller and Davis 1989). Arsenic is adsorbed to and coprecipitates with iron oxyhydroxides which are rapidly formed upon contact with the stream (Fuller and Davis 1989). The locations of some groundwater seeps are clearly visible by orange iron oxide precipitates covering the streambed.

Sample Collection

The immature stages (larvae, nymphs, and pupae) of benthic insects were collected with kick nets and by hand from riffle areas during low flow. Typically at each station, a single riffle was sampled repeatedly over a large area (tens of square metres) until an adequate number of individuals was collected. Aerial adults were collected with a sweep net (Whitewood Creek only). Specific taxa were targeted for collection based primarily on three considerations: wide distribution throughout the study reach, densities relatively high, and individuals relatively large. Additionally, taxa representing different trophic levels were selected.

The Clark Fork River was sampled along a 381-km reach downstream from Warm Springs Creek (Fig. 1). Discharge along this reach increases substantially due to tributary inflows. For example, mean discharge between October 1985 and September 1986 was 7.73 m^3/s near station 34.6 and 208 m^3/s near station 381.1 (Fig. 1). Based on preliminary sampling in 1984 and 1985, six taxa from two orders (Trichoptera and Plecoptera) were selected as bioindicators. These taxa were targeted for collection in August 1986 at 15 locations (Fig. 1). These samples were analysed for Cu, Cd, Pb, and Zn. In 1986, *Hydropsyche* (Trichoptera) was not separated to species. In August 1990, *Hydropsyche* spp. were collected and analysed separately. *Arctopsyche grandis*, another hydropsychid caddisfly, also was collected. Eight of the 15 stations sampled in 1990 were stations sampled in 1986 (Fig. 1). Metal concentrations in Clark Fork insects were referenced against the average metal concentrations in insects collected from two uncontaminated tributaries, Rock Creek and the Blackfoot River (Axtmann and Luoma 1991). Reference samples were collected in August 1986, April 1987, June 1987, August 1987, and August 1989 within 25 km of the confluences of these two tributaries with the Clark Fork (Fig. 1). Concentrations in the reference samples varied little among years. The largest year-to-year difference in concentration observed at either tributary for any taxon was 6 μg Cu/g (dry weight), 0.2 μg Cd/g, 1.5 μg Pb/g, and 45 μg Zn/g.

Whitewood Creek changes from a relatively high-gradient, canyon-confined stream to a lower-gradient, more open, meandering stream with extensive overbank deposits as it flows northeast from the Black Hills to the prairie. Preliminary sampling in 1986 showed that the structure of the benthic community changed along the stream course. Consequently, few species were common to all stations within the study reach. In May–June 1987, 15 taxa from four orders (Ephemeroptera, Trichoptera, Plecoptera, and Hemiptera) were collected at stations 2–6, covering about a 40-km reach below the mine, and analysed for As (Fig. 2). Stations 5 and 6 were located within 200 m of one another to assess influences of localized input of As-laden groundwater on As concentrations in benthic insects. Reference concentrations were based on specimens collected in 1986 and 1987 from three stations: station (R1) located upstream of the mine, Spearfish Creek (SC), and the Belle

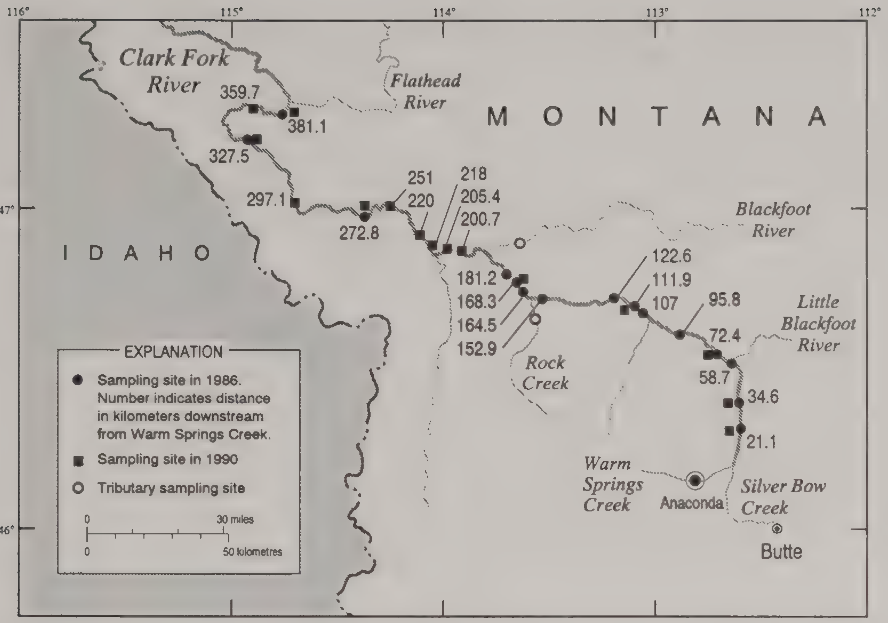
116°
115°
114°
113°
112°
47°
46°
Clark Fork River
Flathead River
M O N T A N A
I D A H O
359.7
381.1
327.5
297.1
272.8
251
220
218
205.4
200.7
181.2
168.3
164.5
152.9
122.6
111.9
107
95.8
72.4
58.7
34.6
21.1
Blackfoot River
Little Blackfoot River
Rock Creek
Warm Springs Creek
Anaconda
Silver Bow Creek
Butte
EXPLANATION
● Sampling site in 1986. Number indicates distance in kilometers downstream from Warm Springs Creek.
■ Sampling site in 1990
○ Tributary sampling site
0
30 miles
0
50 kilometres

FIG. 1. Clark Fork River drainage basin in Montana, USA. Station locations are designated by distance in river kilometres downstream from Warm Springs Creek.

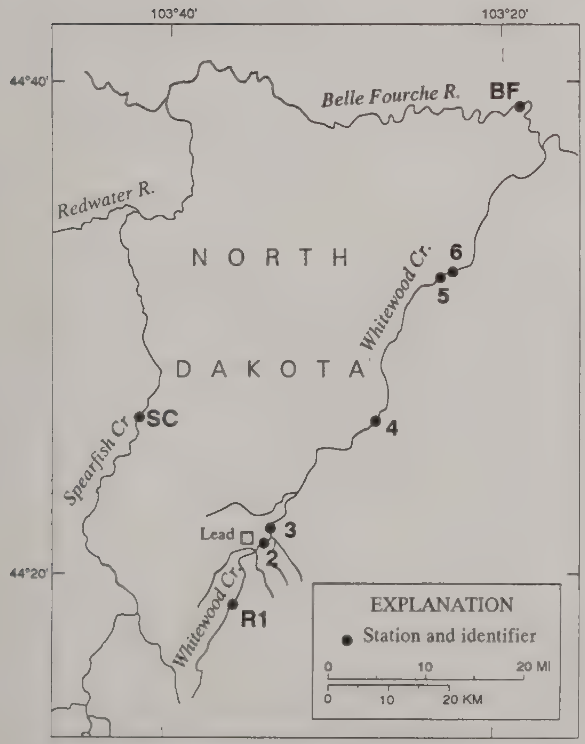
103°40'
103°20'
44°40'
44°20'
Belle Fourche R.
BF
Redwater R.
N O R T H
D A K O T A
Whitewood Cr.
6
5
4
SC
Spearfish Cr.
Lead
3
2
Whitewood Cr.
R1
EXPLANATION
● Station and identifier
0
10
20 MI
0
10
20 KM

FIG. 2. Whitewood Creek, South Dakota, USA, showing stations.

Fourche River (BF) upstream of the confluence of Whitewood Creek (Fig. 2).

Insects collected for trace element analysis from the Clark Fork River and Whitewood Creek were initially sorted on site by taxon and held for 4–6 h in plastic bags filled with ambient river water in a cooler to eliminate the contents of their guts. The river water was then decanted and the insects were frozen. Before freezing, some specimens were removed from the plastic bags and preserved in alcohol for taxonomic identification. The frozen samples were thawed in the laboratory and thoroughly rinsed with deionized water to remove particles from external surfaces. Individuals of the same species or genus were further sorted by size, and similar-sized individuals were pooled to make a sample with a total dry weight of at least 50 mg. Plecopterans were measured from the head to the last abdominal segment. The smaller taxa were sized by eye, and the average dry weight of individuals was determined from the total dry weight and the number of individuals in the composite sample.

Sample Analysis

Samples from the Clark Fork River were dried at 80°C, weighed, and then digested with hot 16 M HNO_3 reflux. The acid was evaporated after the sample solution turned clear, the residue reconstituted in 3 M HCl, and the solution analysed for Cu, Cd, Pb, and Zn by either flame atomic absorption spectrophotometry (AAS) or inductively coupled argon emission spectrophotometry.

Arsenic was deterined in insects from Whitewood Creek. Samples were homogenized in a high-speed tissue homogenizer. The homogenate was freeze-dried, ashed in a muffle furnace at 450°C, reconstituted in 6 M HCl, and analysed by hydride-generation AAS.

Fine-grained bed sediments were collected simultaneously with the insect samples in the Clark Fork River in 1986 and in Whitewood Creek in 1987 following procedures described by Axtmann and Luoma (1991) and Cain et al. (1989). A polypropylene scoop was used to scrape sediment from the surface (0–1 cm) of several deposits in shallow, still water along the water's edge. The sediment was wet-sieved on site with ambient river water through a 60-μm nylon mesh screen. Sediment collected from the Clark Fork River was transported on ice to the laboratory and dried at 80°C. Sediment from Whitewood Creek was allowed to settle for 24 h after collection. The river water was decanted, and the sediment was frozen and later freeze-dried. Dried sediments from both the Clark Fork River and Whitewood Creek were ground to homogeneous powders. Subsamples were extracted wth 0.6 M HCl to estimate the biologically available metal fraction (Langston 1980; Luoma and Bryan 1978, 1981, 1982). Clark Fork River sediments were analysed for Cd, Cu, Pb, Zn, and Fe by flame AAS. Whitewood Creek sediments were analysed for As by hydride-generation AAS.

Quality assurance of the analytical methods was checked with NIST standards. Bovine liver, oyster tissue, and river sediment (NIST standard reference materials 1577a, 1566a, and 1645) were analysed routinely to check the recoveries of Cd, Cu, Pb, Zn, and Fe. Albacore tuna (NIST reference material 50) was run with each group of samples analysed for As. Concentrations for most elements were usually within the 95% confidence limits of the certified mean concentrations. Zinc recoveries from 1577a and 1566a were typically 85–90% of the certified concentrations.

Statistical Analysis

The relationship between bioaccumulation and environmental contamination in the Clark Fork River was assessed by correlating trace metal concentrations in individual taxa with sediment metal concentrations (Table 1). Concentration data were log-transformed for the analysis.

The coefficient of variation was used to characterize the effect of pooling data from related species, as might be employed in a field sampling strategy. Several stations from each river were selected to provide a consistent suite and maximum number of taxa for this analysis (Table 1). Data from these stations were combined to increase the sample size. Stations selected in the Clark Fork River were located between 72.4 and 181.2 km (Table 1). Data from 1986 characterized the variance within hydropsychid caddisflies and stoneflies. Data from 1990 characterized the variance only among three species of hydropsychid caddisflies. Three Whitewood Creek stations were selected because the two major taxa collected in the stream in 1987, Trichoptera and Ephemeroptera, were well represented. Within orders, the median of the coefficients of variation for replicate samples of all species collected at the selected stations was used to characterize the variation in trace element concentration at the species level. For higher taxonomic levels, the mean and coefficient of variation of trace element concentrations for all species within the same genus, family, or order were calculated at each station. The median of the coefficients of variation for all stations characterized the variation within each taxonomic group.

The effects of feeding habit and size on insect element concentrations were evaluated by analysis of covariance (ANCOVA). Although food preferences vary greatly among taxa and may change over the life history of a species, each taxon was assigned to one of four broad feeding categories based on descriptions of trophic relationships in Merritt and Cummins (1984): herbivores, detritivores, omnivores, or predators. The herbivore category included mayflies only. Detritivores comprised the caddisflies *Limnephilus* and *Hesperophylax* and the stonefly *Pteronarcys californica*. The omnivore category comprised several species of hydropsychid caddisflies. The predators included *Rhyacophila, Ambrysus*, and several perlid stoneflies. The ANCOVA included data from several stations (Table 1). Feeding habit was treated as the main factor, and the mean dry weight (size) of individuals in each sample was included as a covariate. The concentration of metals extracted in 0.6 M HCl from fine bed sediments (<60 μm) also was added as a covariate to adjust insect concentrations for differences in metal contamination among stations. Element concentrations and insect dry weights were log-transformed for the analyses. This analysis was limited to stations where at least three different feeding categories were represented in the collections (Table 1). In Whitewood Creek, four feeding categories were represented, but all four were not collected at any station. Therefore, the ANCOVA was run for two separate data sets (Table 1).

Results

Distribution of Taxa

The availability of species for trace element analysis differed among stations in both the Clark Fork River and Whitewood Creek. Of the six taxa targeted for collection in the Clark Fork River, only *Hydropsyche* spp. and *Isogenoides* sp. were collected at stations upstream of 60 km (Table 2). All of the targeted taxa were found between 61 and 191 km, although

TABLE 1. Summary of the data used in the different analysis of factors affecting bioaccumulation in insects. Feeding categories for ANCOVA: H = herbivore; D = detritivore; O = omnivore; P = predator.

Analysis	River	Year	Stations	Approach
Bioaccumulation vs. sediment contamination	Clark Fork	1986	15-stn. transect (21–381 km)	Correlation
Variation within taxa	Clark Fork	1986	72.4, 107, 164.5, 181.2	Coefficient of variation
	Clark Fork	1990	72.4, 111.9, 168.3	
	Whitewood Cr.	1987	2–4	
Effect of feeding habit and size	Clark Fork	1986	72.4, 107, 164.5, 181.2	ANCOVA: D, O, P
	Whitewood Cr.	1987	R1–3	ANCOVA: H, D, P
	Whitewood Cr.	1987	2–6	ANCOVA: H, O, P

TABLE 2. Distributions of benthic insects collected (+) for trace element analysis in the Clark Fork River, Montana, in August 1986, Whitewood Creek, South Dakota, in May–June 1987, and reference sites. "−" means the taxon was not collected because it was either rare or absent. All locations given in river kilometres except reference sites.

Taxon	Reference	Clark Fork River reaches (km)					Whitewood Creek station ID and location (km)				
		0–60	61–106	107–164	165–191	192–381	2 0	3 1	4 20	5 38	6 38.2
Trichoptera											
Hydropsyche spp.	+	+	+	+	+	+					
Arctopsyche grandis	+	−	+	+	+	+					
Plecoptera											
Claassenia sabulosa	+	−	+	+	+	+					
Hesperoperla pacifica	+	−	+	+	+	−					
Isogenoides sp.	+	+	+	+	+	−					
Pteronarcys californica	+	−	+	+	+	−					
Ephemeroptera											
Baetis tricaudatus	+						+	+	+	−	−
Choroterpes sp.	−						−	−	−	+	+
Ephemerella inermis	+						+	+	−	−	−
Tricorythodes sp.	−						−	−	−	+	+
Trichoptera											
Hesperophylax occidentalis	+						−	−	−	−	−
Limnephilus sp. and *Hesperophylax* sp.	−						+	+	−	−	−
Cheumatopsyche spp.	−						−	−	+	+	−
Hydropsyche bronta	−						−	+	+	+	−
Hydropsyche oslari	+						−	−	−	−	−
Hydropsyche slossonae and *oslari*	−						−	−	−	+	+
Hydropsyche spp.	+						+	+	+	−	−
Rhyacophila acropedes group	+						+	+	−	−	−
Plecoptera											
Isoperla quinquepunctata	−						−	−	+	−	−
Hesperoperla pacifica	+						+	−	−	−	−
Hemiptera											
Ambrysus sp.	−						−	−	−	+	+

some species were rare at some stations within this reach (Table 2). Below 191 km the densities of several stoneflies were insufficient for a trace metal sample. Specimens of all targeted taxa were collected in the tributaries. Taxa collected in Whitewood Creek appeared to reflect habitat differences between the upper and lower segments of the stream. Many of the taxa collected in the upper 30-km reach were replaced downstream by other taxa (Table 2). Seven of the 15 taxa were collected from at least one of the reference stations. Eight taxa were not available at any of the reference stations.

Bioaccumulation Related to Sediment Contamination

Trace element concentrations in all taxa in the Clark Fork River were elevated relative to reference samples and thus reflected contamination of the river (Table 3). Contamination in sediments and in most taxa progressively declined downstream (Table 3). Elevated Cu and Cd concentrations were still present in all taxa 191–381 km downstream of the origin of contamination. Metal-specific differences in bioaccumulation among taxa in the Clark Fork were apparent from differences in concentrations at the same stations, contrasting patterns in the downstream distributions of contaminants, and differences in correlations with metals in the sediments. Normalizing sediment metal concentrations to Fe concentrations in the sediments (e.g. Luoma and Bryan 1978; Langston 1980) had little affect on correlations between sediment metal concentrations and metal bioaccumulation.

Copper and Cadmium

Copper concentrations differed among taxa by a factor of about 2 at reference stations and by a factor of 3.5 within each reach in the Clark Fork (Table 3). Concentrations in hydropsychid caddisflies decreased downstream (Fig. 3a). Copper in *Hydropsyche* spp. and in *Arctopsyche grandis* correlated significantly with Cu in sediments (Table 4). Copper accumulation by *Hydropsyche cockerelli* and *Hydropsyche occidentalis* was virtually the same where these species were collected together in 1990 (Fig. 3a). Differences were evident between *H. occidentalis* and a third species at the two most upstream stations (Fig. 3a). However, Cu in these *Hydropsyche* spp. was typically twice that found in *A. grandis* in both 1986 and 1990 (Fig. 3). Differences in Cu concentrations and downstream patterns also occurred among stoneflies (Fig. 4). *Pteronarcys californica* was collected at only eight stations in the Clark Fork. At most of these stations, Cu concentrations in this species were higher than those in either of the other two species of stonefly or in *Hydropsyche* spp. Copper concentrations in *P. californica* decreased downriver, but tissue concentrations were not correlated significantly with Cu in sediments (Table 4). The insignificant correlation may be attributed to the species' relatively narrow distribution (samples were collected from only eight

TABLE 3. Trace metal concentrations (mean ± 1 SD, μg/g dry wt.) in insects and sediments from the Clark Fork River in August 1986 and from reference sites. Samples were collected at three stations within the specified reach except for *Hesperoperla* sp. ($n = 1$). "–" means the taxon was not collected because it was either rare or absent.

Element	Taxon	Reference	Reach		
			0–60	106–164	191–183
Copper	Trichoptera				
	Hydropsyche spp.	18 ± 4	204 ± 18	72 ± 8	27 ± 5
	Arctopsyche grandis	11 ± 2	–	33 ± 4	20 ± 2
	Plecoptera				
	Pteronarcys californica	32 ± 3	–	115 ± 6	–
	Claassenia sabulosa	34 ± 11	–	68 ± 0.3	51 ± 3
	Hesperoperla pacifica	28 ± 3	–	46	–
	Isogenoides sp.	16	84 ± 8	68 ± 4	–
	Sediment	18 ± 5	779 ± 228	408 ± 103	129 ± 53
Cadmium	*Hydropsyche* spp.	0.2	2.8 ± 0.6	2.2 ± 0.6	0.7 ± 0.2
	Arctopsyche grandis	0.2 ± 0.1	–	1.4 ± 0.3	0.6 ± 0.1
	Pteronarcys californica	0.1 ± 0.1	–	1.0 ± 0.1	–
	Claassenia sabulosa	0.1	–	1.4 ± 0.1	0.6 ± 0.03
	Hesperoperla pacifica	0.2 ± 0.1	–	1.0	–
	Isogenoides sp.	<0.4	1.8 ± 0.2	1.4 ± 0.3	–
	Sediment	<0.3	6.6 ± 1.5	3.5 ± 0.9	1.6 ± 0.3
Lead	*Hydropsyche* spp.	1.8 ± 2.2	12.8 ± 1.5	8.1 ± 1.3	3.1 ± 0.9
	Arctopsyche grandis	1.2 ± 1.1	–	4.1 ± 0.4	2.1 ± 0.3
	Pteronarcys californica	0.6 ± 0.4	–	7.4 ± 1.3	–
	Claassenia sabulosa	<0.1	–	0.4 ± 0.1	0.4 ± 0.2
	Hesperoperla pacifica	<0.2	–	1.0	–
	Isogenoides sp.	<0.4	2.6 ± 1.5	1.2 ± 0.4	–
	Sediment	11 ± 1	125 ± 40	90 ± 22	40 ± 3
Zinc	*Hydropsyche* spp.	112 ± 2	270 ± 36	233 ± 20	122 ± 22
	Arctopsyche grandis	136 ± 8	–	191 ± 9	134 ± 1
	Pteronarcys californica	183 ± 20	–	253 ± 9	–
	Claassenia sabulosa	177 ± 19	–	238 ± 14	200 ± 5
	Hesperoperla pacifica	311 ± 42	–	387	–
	Isogenoides sp.	288	328 ± 8	357 ± 10	–
	Sediment	54 ± 1	1073 ± 337	894 ± 179	354 ± 73

stations) and the variability in the tissue concentrations among stations. Concentrations of Cu in *Isogenoides* sp. also showed a detectable decrease downstream which correlated with sediment Cu concentrations (Table 4). In contrast, concentrations of Cu in *Claassenia sabulosa* changed little over 320 km (Fig. 4), although concentrations were significantly higher throughout the Clark Fork than at reference stations. *Claassenia sabulosa* was not found in the upper 60 km. Downstream trends in other species were more obvious because of the high tissue concentrations in this reach.

Cadmium concentrations in most taxa in the upper 164 km of the Clark Fork exceeded concentrations in reference populations by an order of magnitude (Table 3). Differences in concentrations among taxa within a given reach were generally less than twofold. The highest concentrations occurred in *Hydropsyche* spp. (Table 3). Differences in Cd accumulation were evident between *Hydropsyche* spp. at the three most upstream stations where contamination was greatest, but not at the rest of the stations (Fig. 5a). Cadmium contamination in *Hydropsyche* spp. was also greater than in *A. grandis* at the most contaminated stations in the river in 1986 (Fig. 5b), but differences between the two caddisflies were less under less contaminated conditions (e.g. in 1990 when concentrations were about half of those in 1986; Fig. 5). Concentrations of Cd in the caddisflies correlated significantly with sediment Cd concentrations (Table 4). In the plecopterans, Cd in *Isogeniodes* sp. and in *C. sabulosa* showed a small downstream decrease (data not shown) which correlated significantly with sediment concentrations (Table 4). Concentrations of Cd decreased downstream in *P. californica*, but did not correlate significantly with sediment concentrations (Table 4) because of variability in the data similar to that observed with Cu.

Lead and Zinc

The differences in Pb concentrations among taxa from uncontaminated and contaminated stations exceeded an order of magnitude (Table 3). Concentrations of Pb in *Hydropsyche* spp. and *A. grandis* reflected the downstream decrease in Pb concentrations in sediments (Table 3). Lead in stoneflies was not significantly correlated with Pb in sediments (Table 4), although Pb in *P. californica* decreased from 40 μg/g at 72 km to 4 μg/g at 181 km.

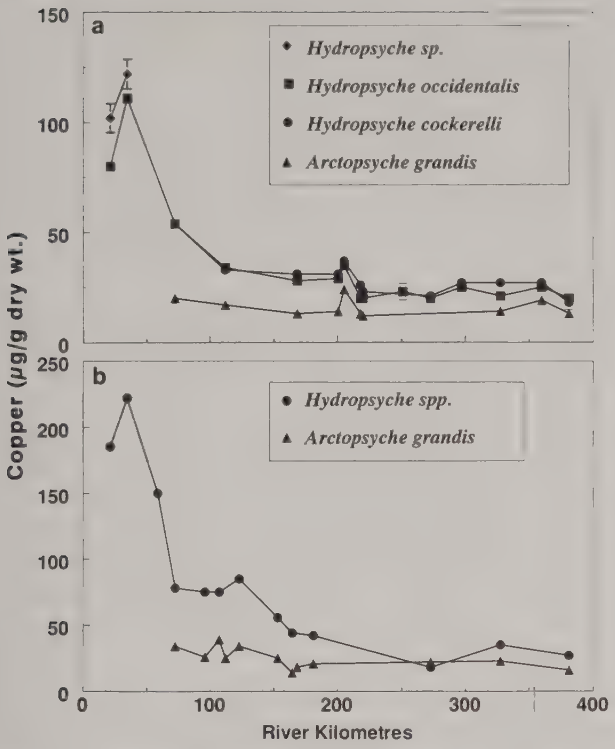

FIG. 3. Downstream distributions of Cu concentrations in hydropsychid caddisflies in the Clark Fork River in (a) 1990 and (b) 1986. Concentrations are for composite samples (n = 1–7). Error bars are ±1 SE of the mean concentration.

Zinc concentrations varied by a factor of 2–3 among taxa at reference and contaminated stations (Table 3). Zinc concentrations in sediments correlated with Zn in trichopterans but not in plecopterans (Table 4). However, all taxa were less responsive to Zn contamination than other metals. For example, Zn in *Hydropsyche* spp. in the 0- to 60-km reach exceeded reference concentrations by only a factor of 2.4 (Table 3). In the same reach, Zn in *Isogenoides* sp. was only 1.1 times greater than reference concentrations.

Arsenic

In Whitewood Creek, As concentrations were elevated downstream of the mine at stations 2–4 in all taxa that could be compared with reference populations (Table 5). However, the details of the downstream trends were difficult to assess because no single species was available at all stations. Differences in As between stations 5 and 6 appeared to reflect important localized processes. High As concentrations were found in sediments and in *Choroterpes*, *Tricorythodes*, and *Ambrysus* collected at station 6 within the plume of a groundwater seep which was marked by the iron oxide stain on the stream bottom. In contrast, concentrations were lower in these taxa and sediment collected approximately 200 m upstream at station 5. At station 6, *Hydropsyche* sp. were collected near midchannel and outside the boundary of the plume. This slight difference in location probably explains why concentrations in this taxon were similar between stations 5 and 6.

Arsenic concentrations differed among taxa from reference areas by an order of magnitude (Table 5). A similar level of variation was observed among taxa from contaminated stations, although concentrations were higher. In general, As concentrations in mayflies and caddisflies were higher than in stoneflies and *Ambrysus* sp. (Table 5). This was the only consistent difference in As concentrations that appeared related to taxonomy.

Effects of Aggregating Data by Taxonomic Level

The variance in trace element concentrations usually increased as data for species were systematically aggregated by genus, family, and order (Fig. 6). Combining data for *Hydropsyche cockerelli* and *H. occidentalis* from the Clark Fork River increased the median coefficient of variation at the genus level for Cd, Pb, and Zn, although the differences in concentrations of these metals between the species were small (e.g. see Fig. 3a, 5a). Including *A. grandis* and aggregating all data at the family level (Hydropsychidae) further increased the coefficient of variation for Pb and Cu. The variance in bioaccumulation data in Trichoptera in Whitewood Creek and in Plecoptera in the Clark Fork River also increased as species were grouped by family and order (Fig. 6). The median coefficient of variation for As in four mayfly species in Whitewood Creek increased slightly from 28 to 34% when the species were combined at the order level. The increase in variance from species to order was greater for Pb, Cu, and As than for Cd and Zn (Fig. 6). Lead in stoneflies in the Clark Fork and As in caddisflies in Whitewood Creek were especially variable.

Influence of Feeding Habit on Bioaccumulation

Feeding habit had a clear influence on concentrations of Pb in insects from the Clark Fork (ANCOVA, Table 6). At the four stations analysed, the average Pb concentrations were highest in the detritivore, intermediate in omnivores, and low-

TABLE 4. Correlation of whole-body insect metal concentrations and acid-extractable (0.6 M HCl) metal concentrations in bed sediment for samples collected from the Clark Fork River in August 1986. Correlation coefficients, r, and sample sizes (in parentheses) are shown. Significance levels: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Taxon	Copper	Cadmium	Lead	Zinc
Trichoptera				
Hydropsyche spp.	0.86 (13)***	0.71 (13)**	0.74 (13)**	0.74 (13)**
Arctopsyche grandis	0.63 (12)*	0.84 (12)***	0.61 (12)*	0.69 (12)*
Plecoptera				
Claassenia sabulosa	0.53 (12)	0.69 (12)*	0.26 (12)	0.53 (12)
Hesperoperla pacifica	0.00 (7)	−0.63 (7)	0.69 (5)	0.43 (7)
Isogenoides sp.	0.74 (12)**	0.66 (12)*	0.36 (11)	0.25 (12)
Pteronarcys californica	0.68 (8)	0.51 (8)	0.66 (8)	0.37 (8)

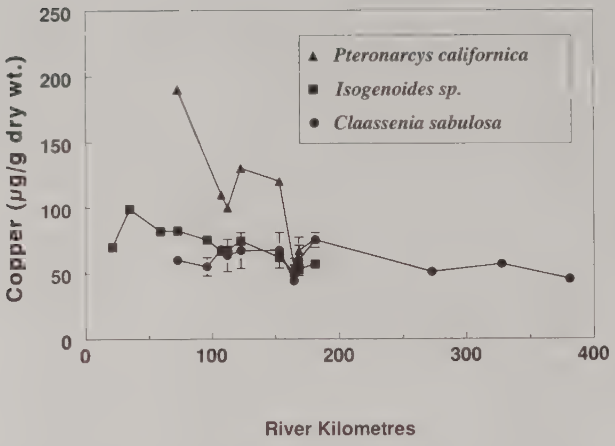

FIG. 4. Downstream distributions of Cu concentrations in stoneflies in the Clark Fork River in1986. Concentrations are for composite samples (n = 1–4). Error bars are ± 1 SE of the mean concentration.

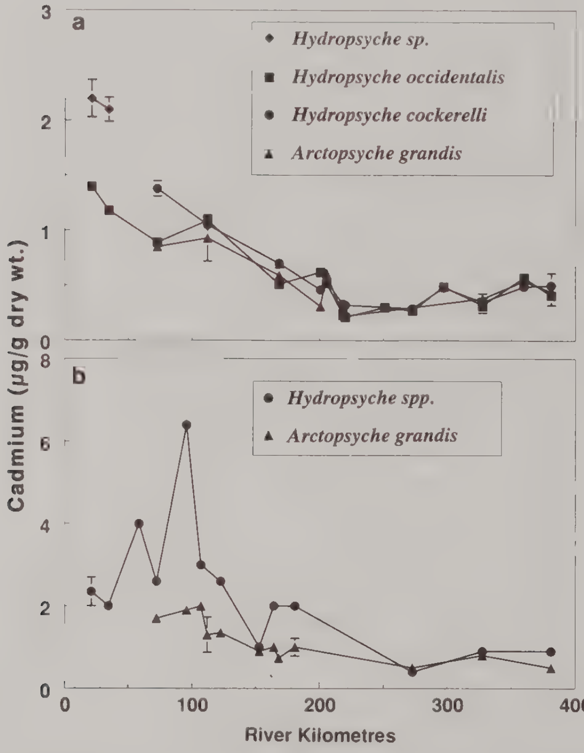

FIG. 5. Downstream distributions of Cd concentrations in hydropsychid caddisflies in the Clark Fork River in (a) 1990 and (b) 1986. Concentrations are for composite samples (n = 1–7). Error bars are ± 1 SE of the mean concentration.

est in predators (Table 7). Feeding habit also may have contributed to the high Cu concentrations observed in the detritivore *P. californica*. Other differences (e.g. Cd) between feeding categories in the Clark Fork were relatively small (Table 7), although some were statistically significant (Table 6). In some instances, differences in concentrations among taxa within a feeding category were as great as differences observed between feeding groups. For example, Zn concentrations in *C. sabulosa* were more similar to those in *P. californica* and *Hydropsyche* spp. than to those in the other two predaceous stoneflies (Table 7).

As with taxonomic level, differences among feeding categories in the Clark Fork were greatest where contamination was highest and diminished as contamination levels approached background. For example, Cu concentrations were 190 µg/g in the detritivore *P. californica* at 72 km (Table 7). At the same station, Cu in omnivores and predators averaged 56 and 61 µg/g, respectively. At 164 km where contamination was lowest among the four stations, concentrations were 55 µg/g in the detritivore and averaged 29 µg/g in the omnivores and 43 µg/g in the predators (Table 7). Differences in Pb concentrations between *P. californica* and omnivores also were less at 164 km than at 72 km.

Results from the ANCOVA suggested that feeding habit might differentiate bioaccumulation among some species within higher taxonomic groups. For example, characterizing Plecoptera by feeding category separated *P. californica* from the predaceous stoneflies (*C. sabulosa, Hesperoperla pacifica,* and *Isogenoides* sp.) and helped explain differences in Pb and Cu concentrations within that order. On the other hand, differences in metal accumulation between the filter-feeding omnivores *Hydropsyche* spp. and *A. grandis* were not explained by feeding category.

The influence of feeding habit on As concentrations was not clear. Feeding category was not a significant factor in differences in As concentrations among taxa representing herbivores, detritivores, and predators at stations R1, 2, and 3, but significant differences were detected among herbivores, omnivores, and predators at stations 2–6 (Table 6). Arsenic concentrations in the predators at these stations were low relative to herbivores and omnivores. However, the effect of feeding habit was difficult to separate from the effect of size (see below).

Effect of Size on Bioaccumulation

Most differences in metal concentrations among taxa from the Clark Fork River did not appear to result from differences in dry weight (size) (Table 6). In the subset of data analysed by ANCOVA, the mean dry weight of individual specimens for all taxa ranged over more than an order of magnitude; however, dry weight only had a significant effect on Cu. A significant interaction between feeding habit and dry weight was detected for Cu and Cd: concentrations in omnivores decreased as dry weight increased. This was a result of differences in metal concentrations between *Hydropsyche* spp. and *A. grandis*. Concentrations of all metals (including Pb and Zn, although these were not statistically significant) in the smaller *Hydropsyche* spp. were typically 2 times greater than in *A. grandis*.

Arsenic concentrations both within and among insect taxa from Whitewood Creek were negatively related to dry weight. For example, As concentrations in all taxa collected at stations R1, 3, and 6 correlated significantly ($p < 0.05$) with the average dry weight of insects composing the samples (Fig. 7) even though the species composition of the community changed from station R1 to station 6. Much of the variation in As concentration among taxonomic groups could be accounted for by differences in the insects' dry weights (sizes). Further, the relative sizes of taxa within different feeding categories may have influenced the statistically detectable effect of feeding habit on As concentrations. Predators were typically the largest specimens collected and had low As concentrations. Herbivores and omnivores were generally small and had high As concentrations.

TABLE 5. Arsenic concentrations (mean ± 1 SD, $n = 1$–9 composite samples, μg/g dry wt.) in insects and sediments from Whitewood Creek, South Dakota, in May–June 1987 and from reference sites. The caddisflies *Limnephilus* sp. and *Hesperophylax* sp. were not separated before As determination. "–" means the taxon was not collected because it was either rare or absent.

		Station				
Taxon	Reference	2	3	4	5	6
Ephemeroptera						
Baetis tricaudatus	10	65 ± 15	80 ± 15	24 ± 2	–	–
Choroterpes sp.	–	–	–	–	156 ± 28	278 ± 86
Ephemerella inermis	16 ± 0.2	40 ± 1	59 ± 28	–	–	–
Tricorythodes sp.	–	–	–	–	92 ± 20	625 ± 80
Trichoptera						
Hesperophylax occidentalis	6 ± 3	–	–	–	–	–
Limnephilus sp. and *Hesperophylax* sp.	–	8	10 ± 0.03	–	–	–
Cheumatopsyche spp.	–	–	–	56 ± 8	59	–
Hydropsyche						
H. slossonae oslari	7 ± 3	58 ± 10	37 ± 6	98 ± 26	–	–
H. bronta	–	–	20	80 ± 4	29	–
H. sp.	2 ± 1	–	–	–	–	–
H. sp.	–	–	–	–	66 ± 25	77 ± 15
Rhyacophila sp.	1 ± 1	4	64	–	–	–
Plecoptera						
Isoperla quinquepunctata	–	–	–	10 ± 4	–	–
Hesperoperla pacifica	2 ± 1	5 ± 1	–	–	–	–
Hemiptera						
Ambrysus sp.	–	–	–	–	25 ± 5	73 ± 42
Sediment	18 ± 4	84 ± 1	145 ± 7	440 ± 18	660 ± 4	764 ± 74

Size differences within taxa could bias comparisons of metal contamination between stations at Whitewood Creek. For example, individual *Hesperophylax* sp. with an average dry weight of 7 mg at reference station R1, above the mine, had As concentrations only slightly lower than those in larger specimens of *Hesperophylax* sp. and *Limnephilus* sp. (average dry weight of 44 mg) at station 3 located below the mine (Fig. 7). From this comparison alone one might wrongly conclude that station 3 was not contaminated.

Arsenic Contamination of the Exoskeleton

The strong size effect on As concentrations in insects from Whitewood Creek suggested that As was associated with the exoskeleton of the larvae and nymphs. Arsenic concentrations in pupae and adult specimens from Whitewood Creek were only 15–50% of the As concentration in larvae and nymphs (data not shown). Cessation in feeding and/or the loss of the gut and its contents during metamorphosis could have affected the As concentrations in pupae. However, the most likely cause for these differences is that the exoskeleton of immature specimens, which is shed during ecdysis and which was intentionally not collected with the pupal samples, was enriched with As relative to internal tissues. Arsenic body burdens (micrograms) were calculated from the average insect dry weight and As concentrations for the different developmental stages. These results were used to estimate the total amount of As in the larvae or nymph exoskeleton (assuming that the differences in As among life stages were entirely due to As sorbed to the exoskeleton). Arsenic associated with the exoskeleton ranged from 32% of the total body burden in taxa collected above the mine to 56–99% at stations below the mine (Table 8).

Arsenic-bearing particles appeared to contribute to the surface contamination of Whitewood Creek insects. Scanning electron microscopy – energy dispersive X-ray analysis (SEM–EDX) showed that the external surfaces of specimens were littered with inorganic particles (Fig. 8), despite repeated rinsing with deionized water prior to As analysis. The particles appeared to be simply trapped by setae. The particles on the insect surfaces were similar in character to As-enriched iron oxyhydroxides that precipitate when contaminated groundwater is discharged into Whitewood Creek (Fuller et al. 1988). In those particles on the insects in which As was detected, Fe was the major constituent (Fig. 9). The As/Fe molar ratio of iron oxyhydroxides from the stream (Fuller et al. 1988) was similar to the As/Fe molar ratio in insects (Cain et al. 1988). Iron particles also were observed in the gut cavity, but with much lower frequency than on the exoskeleton. In only one case (a specimen of the filter-feeding *Hydropsyche* sp.) did an Fe particle in the gut have detectable concentrations of As.

Discussion

The concentrations of trace contaminants in the bodies of all benthic insects in the Clark Fork River and Whitewood Creek were elevated where sediments were contaminated, indicating that bioaccumulation is a general, community-level response to contamination in these lotic environments. Thus, analysis of tissues from any member of the benthic insect community might be used to detect exposure to contaminants. However, taxa differ in their suitability as bioindicators because of differences in distribution within study reaches and differences in bioaccumulation.

Changes in the composition of the benthic community prevented direct comparisons of As contamination in any one species among all stations in Whitewood Creek or between contaminated and reference stations. Differences in community composition were probably caused by changes in stream con-

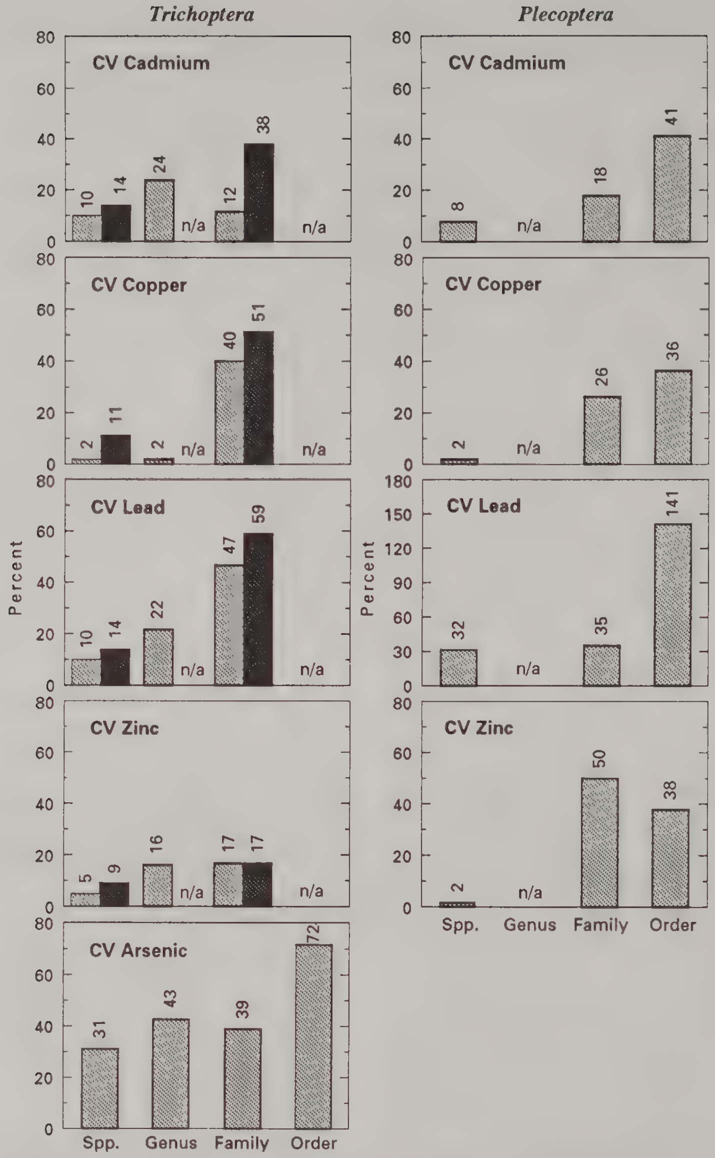

FIG. 6. Coefficients of variation (%) for trace element concentrations within different taxonomic groups. Each value is the median of the coefficients of variation for several stations in the Clark Fork River and in Whitewood Creek. Spp. is the median coefficient of variation for replicate ($n > 1$) composite samples of species. Values for higher taxonomic levels resulted from aggregating concentration data of all species within the specified taxon. Cadmium, Cu, Pb, and Zn data are from the Clark Fork River. Trichoptera are represented by Hydropsychidae, exclusively. Dark bars are for 1986 and light bars are for 1990. Arsenic data are from Whitewood Creek. "n/a" means taxa were not available for grouping at that level.

ditions and the character of the benthic habitat (Cain et al. 1988). In the Clark Fork River, changes in the structure of the benthic community appeared to be related to the effects of the pollution (Chadwick and Canton 1986; McGuire 1988, 1989). In the upper 60-km reach, densities of many taxa including mayflies and stoneflies are significantly lower than farther downstream, and some taxa (e.g. *C. sabulosa* and *P. californica*) are absent. Downstream, more species are represented in the assemblage, although population densities of species vary among stations (McGuire 1988, 1989; pers. obs.). Because of their wide distribution and relatively high densities, *Hydropsyche* spp. were better than other taxa for assessing metal contamination over broad spatial scales.

Trace element bioaccumulation is typically species dependent, but similarities may exist among groups of related species. For example, concentrations of trace metals may be higher in mayflies than in other taxa (Nehring 1976; Burrows and Whitton 1983; Besser and Rabeni 1987; Hatakeyama et al. 1988). Differences (or similarities) in bioaccumulation have been explained by functional and morphological characteristics. Feeding habit was cited as a cause of differences in trace element accumulation among insect species (Elwood et al. 1976;

TABLE 6. ANCOVA probability levels for the effects of feeding habit, size (dry weight), and contamination (sediment metal concentration) on trace element concentrations in insects; ns means not significant at $p \leq 0.05$. Data for Cd, Cu, Pb, and Zn are from four stations in the Clark Fork River where taxa representing three feeding categories (detritivore, omnivore, and predator) were collected in August 1986. Data for As are from stations in Whitewood Creek sampled in May–June 1987.

	Cd	Cu	Pb	Zn	As[a]	As[b]
Factor						
Feeding habit	0.013	0.017	0.000	0.000	ns	0.018
Covariate						
Dry weight	ns	0.016	ns	ns	0.016	0.012
Contamination	ns	0.000	0.031	ns	0.000	0.000
Interaction						
Feeding × weight	0.028	0.001	ns	ns	ns	ns
Feeding × contamination	ns	0.009	ns	ns	ns	ns

[a] Includes detritivores, herbivores, and predators from stations R1–3.

[b] Includes herbivores, omnivores, and predators from stations 2–6.

TABLE 7. Trace metal concentrations in insects having different feeding habits. Values in bold are the averages of concentrations in composite samples collected at four stations in the Clark Fork River in 1986 where all feeding categories were present (Table 1). The minimum and maximum concentrations in individual taxa from the four stations are shown in parentheses.

Feeding category	Cu	Cd	Pb	Zn
Detritivore	**102**	**1.1**	**14.1**	**234**
Pteronarcys californica	(55–190)	(0.2–2.8)	(2.5–39.8)	(208–248)
Omnivore	**43**	**1.9**	**4.5**	**198**
Hydropsyche spp.	(44–78)	(2.0–2.6)	(1.8–8.0)	(221–234)
Arctopsyche grandis	(14–34)	(1.0–1.7)	(1.8–3.0)	(172–185)
Predator	**54**	**1.2**	**0.8**	**338**
Claassenia sabulosa	(44–60)	(1.6–1.7)	(0.1–2.1)	(209–248)
Hesperoperla pacifica	(36–42)	(1.2–2.1)	(0.2–0.6)	(471–483)
Isogenoides sp.	(50–82)	(0.8–1.1)	(0.3–1.7)	(335–342)

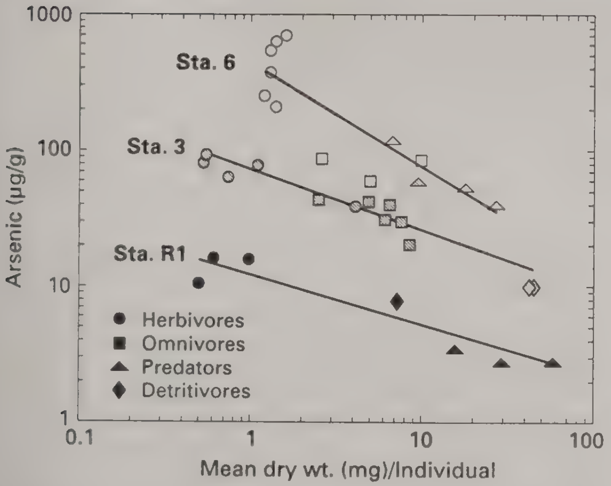

FIG. 7. Arsenic concentrations in taxa from stations R1, 3, and 6 in Whitewood Creek as a function of the insects' dry tissue weights. Each symbol is a single composite sample. Different symbol shading indicates different stations.

Smock 1983b). Some authors have suggested that the lowest trace element concentrations occur in predators (Nehring 1976; Burrows and Whitton 1983; Smock 1983b; Timmermans et al. 1989), and insects that ingest sediments may have exceptionally high concentrations of some elements (Smock 1983b). The latter may result from concentrations of metals associated with undigested material in the digestive tract (Elwood et al. 1976; Smock 1983b; Hare et al. 1989). The external body surface also may be an important site of metal accumulation in insects (Elwood et al. 1976; Smock 1983b; Krantzberg and Stokes 1988; Cain et al. 1989; Timmermans and Walker 1989; Gower and Darlington 1990; Hare et al. 1991; van Hattum et al. 1991), thus creating a size dependence on concentrations. Bioaccumulation of essential and nonessential trace elements may differ. Chironomids appear to regulate Zn and Cu in contaminated lakes, but not Cd and Pb (Krantzberg and Stokes 1989).

In this study, examples of all of the influences cited above were evident, but these effects were element specific, species specific, and influenced by the hydrogeochemical nature of the contamination. Bioaccumulation of Pb was clearly influenced by feeding habit, with concentrations highest in a detritivore and lowest in predators. However, this pattern of accumulation was not consistent with other elements. Copper concentrations were highest in a detritivore where sediments were highly contaminated in the Clark Fork, but where contamination was less severe, the concentrations were similar to those in other taxa. Feeding habit had no discernable influence on Cd and Zn bioaccumulation. The size of individuals clearly influenced As concentrations in Whitewood Creek because of the contamination of external surfaces of the body. Hare et al. (1991) reached a similar conclusion for As in a lake-dwelling insect. In Whitewood Creek the exoskeleton was contaminated with As-enriched iron oxides which are produced from acidic groundwater inflows. Localized areas of exceptional As contamination

TABLE 8. Arsenic content (average μg/individual ±1 SD, $n = 1$–5) in larva, nymph, pupa, and adult specimens in Whitewood Creek. The percent As associated with the larva/nymph exoskeleton was estimated from the difference in As content between those life forms and the pupa and adult phases.

Station	Taxon	Life form			% As in exoskeleton
		Larva/nymph	Pupa	Adult	
R1	*Hesperophylax* sp.	56	38		32
2	*Hesperophylax* sp. and *Limnephilus* sp.	134	58		57
3	*Hesperophylax* sp. and *Limnephilus* sp.	436 ± 11	194 ± 41		56
	Rhyacophila sp.	606	17		97
4	*Isoperla* sp.	55 ± 11		2 ± 1	96
	Hydropsyche spp.	386 ± 68		5 ± 0.1	99

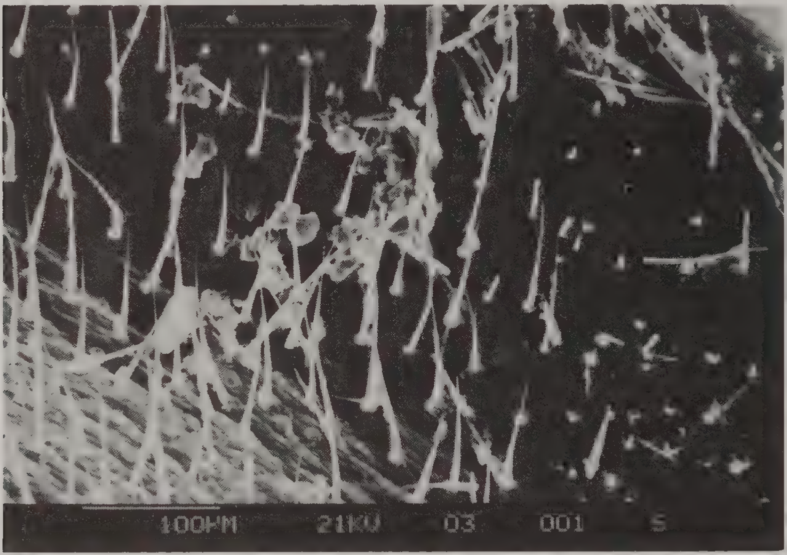

FIG. 8. Scanning electron micrograph of particles (oval and irregularly shaped objects near center of field) among setae of a specimen of *Hesperoperla pacifica* collected from station 2 in Whitewood Creek.

were common in this system where groundwater seeps contacted the stream channel. Size was not generally important in interpreting metal concentrations in insects from the Clark Fork River, where acid inflows are not common. Size appeared to be an important consideration for comparisons only between *Hydropsyche* spp. and *A. grandis*. However, *A. grandis* is more predaceous and ingests larger particles than *Hydropsyche* spp. (Wiggins 1977), and therefore, differences in food selection also could have influenced bioaccumulation of trace metals in these taxa. Insects accumulated Zn the least of all the elements in response to sediment contamination in the Clark Fork River. Physiological regulation of Zn may explain this observation. Copper regulation was not evident in any species, except perhaps *C. sabulosa*. In this species, Cu concentrations throughout the Clark Fork were higher than reference concentrations, but changed little over more than 300 km of the river despite a significant change in sediment Cu contamination.

These examples illustrate the complexity of contaminant accumulation in stream benthos. Bioaccumulation is the result of biotic and abiotic processes whose relative importance in determining contaminant concentrations may differ from one situation to another.

Consideration of the processes that affect bioaccumulation may help direct strategies for effectively using benthic insects as biomonitors in lotic environments. Because the size, age, or developmental stage of individuals can affect concentrations, these factors should be considered. Where concentrations are size dependent, station comparisons are best made with data that account for differences in insect size. Concentrations of contaminants derived from whole-body analysis may also reflect contamination from sediments and food in the gut. The influence of undigested material would probably be greatest for taxa that ingest sediments (Smock 1983b) and in environments where differences in sediment contamination and tissue bioaccumulation are large. In this study, animals lost fecal material during the short depuration period, but complete evacuation of the gut could not be assured. Sediment in the gut may have contributed to the downstream patterns in metal concentrations in some taxa in the Clark Fork River and to differences in metal bioaccumulation among feeding groups. However, ANCOVA

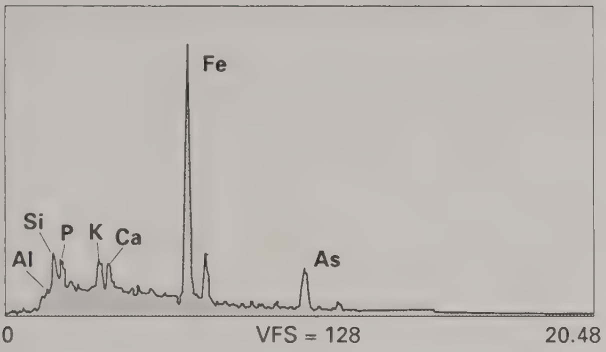

FIG. 9. Energy dispersive X-ray analysis of particle containing Fe and As found on the exoskeleton of a specimen (*Choroterpes* sp.) collected at station 6, Whitewood Creek.

implies that gut content does not affect tissue concentrations of all elements equally. This interpretation is consistent with the direct analysis of the metal concentrations in the gut contents of a burrowing mayfly (Hare et al. 1989) and in *P. californica* from the Clark Fork River (Axtmann et al. 1991). Quantifying the contribution of gut content will be important in determining tissue incorporation of trace elements and the influence of trophic level on bioaccumulation.

This study has demonstrated the difficulty in utilizing a single, cosmopolitan species for biomonitoring cobble-bottom river systems. One strategy for countering this problem would be to combine species for analysis. Our results indicate that this approach would sacrifice precision and sensitivity because of the inherent variability in trace element bioaccumulation among taxa. The problems with combining taxa are most severe at the most contaminated sites, since variability in contaminant concentrations among taxa appears to be greatest in such situations. Changes in species composition among stations also would lead to intractable errors.

Although the increases in variance and the potential biases that result from combining taxa are smaller for some elements than for others, samples should be separated to the lowest taxon practical in order to maximize sensitivity in multielement studies. Ideally, a single species should be compared throughout a study area. In lotic environments, this may be possible over short reaches of a river system, but improbable in studies covering long reaches of a river or an entire basin where a variety of habitats are encountered. Also, species identifications may be difficult to ascertain. In lieu of single species, comparisons of contamination at the genus level appear to be a practical alternative. Differences in trace element concentrations among *Hydropsyche* spp. were relatively small. This may be because the genus comprises ecologically and morphologically similar species (Wiggins and Mackay 1978). If *Hydropsyche* is typical, then grouping species of a genus may be an acceptable compromise to preserve sample precision while reducing analytical costs.

In many cases, it may be necessary to integrate information from several different taxa to assess contamination. Multispecies approaches can be effective in documenting the intensity and extent of contamination in lotic environments (e.g. Moore et al. 1991). When using this approach, taxa should be carefully selected to allow the greatest possible opportunity to make relative comparisons of contamination over space and time.

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Community Response to Cumulative Toxic Impact: Effects of Acclimation on Zinc Tolerance of *Aufwuchs*

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Aufwuchs communities were developed on artificial substrates in a local pond. Second-generation communities were developed on identical substrates in laboratory systems receiving three levels of zinc (Zn): background, 73, and 172 $\mu g \cdot L^{-1}$. After 21 d, second-generation communities were exposed to five concentrations of Zn ranging from background to 10 078 $\mu g \cdot L^{-1}$ for 48 h. Protozoan communities developed under Zn stress were initially less rich taxonomically but subsequently lost fewer species in response to acute Zn exposures. Richness remaining after exposure to high Zn levels ($\geq$2816 $\mu g \cdot L^{-1}$) was similar for all groups. Taxonomic composition changed less in acclimated communities than in the control in response to secondary stress. Gross primary productivity was less impaired by secondary stress in communities acclimated to Zn. Community respiration, algal biomass, total biomass, respiration to biomass ratios, and ratios of soluble to total reactive phosphates did not differ in response to secondary stress. In general, communities developed under Zn stress were initially impaired but changed less in response to additional stress relative to their initial state.

On a fait se développer des communautés biotectoniques sur des substrats artificiels dans un étang. Les communautés de deuxième génération ont été cultivées sur des substrats identiques dans des installations de laboratoire recevant trois concentrations de zinc (Zn) : concentration ambiante, 73 et 172 $\mu g \cdot L^{-1}$. Après 21 jours, les communautés de deuxième génération ont été exposées à cinq concentrations de Zn allant de la concentration ambiante à 10 078 $\mu g \cdot L^{-1}$ pendant 48 h. Les communautés de protozoaires qui se sont développées sous stress causé par Zn étaient au départ moins riches taxinomiquement mais par la suite ont perdu moins d'espèces en réaction à des expositions aiguës de Zn. La richesse restant après exposition à des concentrations élevées de Zn ($\geq$ 2 816 $\mu g \cdot L^{-1}$) était similaire pour tous les groupes. La composition taxinomique a moins changé chez les communautés acclimatées que dans le groupe témoin en réponse au stress secondaire. La productivité primaire brute a été moins affectée par le stress secondaire chez les communautés acclimatées à Zn. La respiration de la communauté, la biomasse algale, la biomasse totale, les rapports de la respiration à la biomassse et les rapports des phosphates solubles par rapport aux phosphates réactifs totaux ne différaient pas dans la réponse au stress secondaire. En général, les communautés qui se sont développées sous stress causé par Zn ont été affectées au départ, mais ont moins changé en réponse au stress additionnel par rapport à leur état initial.

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Communities in streams are subjected to multiple anthropogenic inputs as well as natural stresses such as spates and temperature change. Cumulative impacts can result from interaction of multiple stresses at one time and from sequential stresses over time (Canadian Environmental Assessment Research Council 1988; Gosselink and Lee 1989). While manipulative experiments have been used to address interactions between multiple chemicals (e.g. Calabrese 1991), there have been fewer studies of the interactions of stress over time. Work at the population level has shown that tolerance to toxic stress can increase or decrease with previous exposure (e.g. Cairns et al. 1976; Stockner and Antia 1976; Duncan and Klaverkamp 1983; Weis and Weis 1989; Steadman et al. 1991). In the case of zinc (Zn), Chapman (1985) reported increases in LC50s (the concentration lethal to 50% of test animals) of 2–5 × that of unacclimated fish.

However, changes in the tolerance of whole communities may be difficult to predict from information on individual populations. While the mechanisms by which the tolerance of a population can change include physiological acclimation and genetic selection for resistance, the tolerance of a community of interacting organisms can change through additional mechanisms that are unique to communities. Most obviously, communities can replace sensitive taxa with more resistant ones (i.e. congeneric homotaxis; Hill and Wiegert 1980). Other possible mechanisms include simplifying the structure and function of the community to a state that is more easily maintained in the face of stress (Odum 1985) and sequestering toxicants in one part of the community. It is also possible that simplification resulting from previous stress could decrease subsequent tolerance by reducing functional redundancy in the community (Stokes 1986).

Only a few experiments have examined differences in subsequent tolerance of intact communities developed under stress. DeNoyelles and Kettle (1985) found that phytoplankton communities previously exposed to $\geq$100 μg atrazine·L^{-1} were better able to maintain primary productivity in the face of a subsequent exposure to 100 μg atrazine·L^{-1}. Blanck and Wängberg (1988) found that previously exposed periphyton communities were better able to maintain their relative primary productivity in the face of subsequent arsenate exposure, but tolerance increases were observed only at acclimation concentrations that impaired taxonomic richness, biomass, and net production. We employed *aufwuchs* communities as surrogates of natural systems to evaluate the effect of acclimation of communities on their ability to maintain biological integrity through cumulative Zn stress.

Materials and Methods

Experimental Units

Aufwuchs communities on polyurethane foam (PF) substrates have been used as microcosms to study the effects of toxic substances on ecosystem structure and function (e.g. Ruthven and Cairns 1973; Niederlehner et al. 1985; Pratt and Bowers 1990). These artificial substrates are colonized by protozoans, bacteria, fungi, algae, rotifers, annelids, and occasional insect larvae and crustaceans. Together, the substrate and its inhabitants constitute a complex assemblage with strong internal interactions. These microcosms display diversity, succession, material and energy cycling, and other ecosystem properties yet can be conveniently manipulated in laboratory-scale experiments. Endpoints have focused on ecosystem-level properties that respond to toxic stress (e.g. Odum 1985) yet are related to management goals such as maintenance of biodiversity, productivity, and stability. While functional endpoints are measured on the whole substrate community, the protozoan component of the community was singled out for taxonomic determinations. The protozoans have proven a particularly effective focal point for the analysis of toxic effects for several reasons (Niederlehner et al. 1985): (a) protozoans are trophically diverse, so monitoring one taxonomic group encompasses effects on taxa that are primary producers, detritivores, consumers, and predators; (b) the number of protozoan taxa on these substrates tends to be relatively large, so comparisons of taxonomic structure have sufficient power; and (c) protozoans as a group are unique in their phylogenetic divergence and so are more likely to span the range of tolerances to a toxic substance than other single groups. In support of the representative tolerance of protozoans, Cairns et al. (1988) found that tolerance distributions of the protozoan component of *aufwuchs* communities were comparable with tolerance distributions based on toxicity tests with commonly tested organisms for six chemicals. The People's Republic of China has adopted PF artificial substrate analyses as a primary tool in water quality monitoring (People's Republic of China 1991).

Test Design

Artificial substrates were cut from commercially available bedding foam (6.0 × 5.0 × 3.75 cm), rinsed with 10% HCl, distilled water, and 50% ethanol, and thoroughly rinsed with distilled water. Substrates were tightly tied with cotton twine around their long axis and suspended just below the surface at a 1-m depth in Pandapas Pond, a 195-ha, man-made impoundment in Jefferson National Forest, Montgomery County, Virginia, USA (Table 1). Substrates were colonized for 21 d, retrieved, transported to the laboratory, and acclimated to ambient laboratory temperatures at the rate of 2°C per day for 4 d.

TABLE 1. Physical and chemical characterization of diluent waters. Table entries are means, standard deviations, and number of observations.

Characteristic	Dechlorinated tap water	Pandapas Pond
pH (units)	7.78	7.10
	0.38	0.60
	6	8
Alkalinity (mg·L^{-1})	56.7	13.0
	11.0	6.5
	6	8
Hardness (mg·L^{-1})	73.8	12.6
	14.3	3.7
	6	8
Conductivity (μmho·cm^{-2})	167.5	97.1
	34.0	17.5
	6	3
Nitrate (mg NO_3-N·L^{-1})	1.12	0.17
	0.25	0.14
	6	8
Total phosphate (mg·L^{-1})	0.06	0.34
	0.02	0.34
	6	8
Sulfate (mg·L^{-1})	16.7	5.2
	5.3	2.1
	6	4
Total organic carbon (mg·L^{-1})	0.403	5.210
	0.061	0.450
	6	3
Ca (mg·L^{-1})	18.17	2.07
	3.37	0.72
	6	8
Zn (μg·L^{-1})	1.3	13.3
	0.3	4.3
	7	3

Second-generation communities were developed on identical PF substrates under controlled stress conditions in the laboratory. One field-colonized substrate was suspended in the center of each high-density polyethylene tank (35 × 28 × 15 cm) containing 7.5 L of test media and surrounded by six initially barren PF substrates. Test media consisted of carbon-dechlorinated tap water (Table 1) either unamended or amended with stock solutions of $ZnSO_4 \cdot 7\ H_2O$ to levels previously shown to reduce protozoan species richness by 30 and 50% in chronic exposures (50 and 225 μg Zn·L^{-1}, respectively; Pratt et al. 1987). Media were replaced continuously by peristaltic pump with volume replacement in 2.4 d. Light was provided by four 1.22-m Vita-lite full-spectrum bulbs (color rendering index >90, Durotest Corp.), yielding a photon flux density (400–700 nm) at the water surface of 100 μE·m^{-2}·s^{-1}. Photoperiod was 12 h light and 12 h dark. Ambient water temperatures ranged from 18.0 to 23.0°C.

After 21 d of colonization, second-generation communities were collected and exposed to secondary stress. Five-second-generation substrates were collected from one tank in each acclimation group and randomly assigned to five acute stress levels. Each substrate was placed in a 600-mL borosilicate glass beaker containing 500 mL of dechlorinated tap water either unamended or amended with stock solutions of $ZnSO_4 \cdot 7H_2O$. Substrates were exposed to the secondary stress for 48 h. Each treatment was replicated three times. Replicates were blocked over time with one complete set of acclimation and secondary stress combinations set up each week for three consecutive weeks.

Data Collection

Levels of stress were confirmed analytically in water samples collected at the time acute tests were set up. A 5-mL grab sample was collected from each vessel, placed in an acid-washed, high-density polyethylene vial, and preserved with 0.25% trace pure nitric acid. Container blanks of deionized, distilled water were prepared at the same time. Acid-labile Zn concentrations were determined by flame atomic absorption spectrophotometry.Concentrations are reported as mean measured acid-labile Zn concentration (micrograms per litre) for all test results in this investigation.

Gross primary production (GPP as milligrams of O_2 per litre of substrate contents per 12 h) and community respiration (CR as milligrams of O_2 per litre of substrate contents per 24 h) were estimated from dissolved oxygen (DO) measurements during the last 24 h of the secondary stress. The DO concentrations were determined with a Yellow Springs Instrument DO meter according to manufacturer's instructions. After 24 h of exposure, the surface of the water in the beaker was covered with gas-impermeable plastic film (e.g. Saran Wrap; Giddings and Eddlemon 1978), and the DO content of the water was monitored immediately after the lights were turned on in the morning, immediately after the lights were turned off in the evening, and immediately after the lights were turned on the following morning. Diurnal differences in DO were used to calculate production and respiration (American Public Health Association (APHA) et al. 1989).

After 48 h of exposure to the secondary stress, communities were destructively sampled. Material from the interstices of each substrate was collected by squeezing the substrate over a sterile 250-mL polystyrene sample cup, resubmerging the substrate in the sampled material, and squeezing again to near dryness. Sample volumes recovered from PF substrates in this manner are 87 ± 4% ($N = 5$) of the total displacement volume of the substrate.

Taxonomic richness of protozoan communities was determined within 12 h of sampling by microscopic examination of live samples. Samples settled for 30 min after harvesting. Two drops of material from the bottom of the sample cup were pipetted onto a microscope slide and covered with a No. 1, 22-mm coverglass. The entire coverglass was scanned at 200 and/or 450× total magnification. Protozoans were distinguished to the lowest practical taxon based on gross morphology and behavior (Pascher 1913–27; Kahl 1930–35; Huber-Pestalozzi 1941–68; Deflandre 1959; Lackey 1959; Thompson 1959; Page 1976; Curds 1982; Curds et al. 1983; Lee et al. 1985). Generally, identification to genus or species was possible. If taxonomic identification was uncertain, observations and drawings or photomicrographs were made to ensure consistent identification over the course of the experiment. Subsamples from each sample were examined until an asymptotic number of species was reached. Generally, two subsamples were required and >1000 individuals were identified.

Nontaxonomic responses of substrate communities to stress were also monitored. In vivo fluorescence (IVF) was measured on a Turner Designs fluorometer, expressed as fluorescence units (FU), and used as an index of algal biomass (Lorenzen 1966). Ash-free dry weight (AFDW) was determined by filtering a 10-ml aliquot on a preashed GF/A glass fiber filter, drying at 105°C for ≥24 h, weighing to the nearest 0.01 mg on a Cahn electrobalance, ashing at 500°C for 1 h, wetting the filters, redrying, and reweighing them. AFDW was expressed as milligrams per litre of substrate contents and used as an index of total biomass. Soluble and total reactive phosphate contents of communities were determined (colorometric determinations using the ascorbic acid method; APHA et al. 1989) on samples prepared by filtration or persulfate digestion, respectively.

Additional ratios describing community structure and function were calculated from measured responses. Respiration to biomass ratios were calculated as CR/AFDW and used as a measure of efficiency in energy use (Odum 1985). Production rates were weighted by algal biomass measurements (GPP/IVF) to yield an assimilation ratio (AR; Clark et al. 1980), a measure of the integrity of photosynthetic function. Overall community metabolism was described as net daily metabolism (NDM, i.e. the net change in oxygen over a 24-h period). The ratio of soluble to total phosphorus was used as an index of nutrient retention efficiency in the community, since the proportion of the phosphorus pool in soluble form is most vulnerable to export.

Statistical Analyses

Two types of biologically significant levels were calculated to compare the resistance of acclimation groups. Lowest observable effect concentrations (LOECs) were identified using ANOVA and Duncan's multiple range tests to compare each secondary stress level with its own control separately for each acclimation group. Day of replication was used as a blocking factor. Where response changed in a relatively uniform direction with increases in concentration, regression analysis was used to fit concentration–effect models (e.g. Stephan and Rogers 1985). Control data were not used in deriving the concentration–effect model. Differences in concentration–effect models between acclimation groups were identified using dummy variable analyses (Kleinbaum and Kupper 1978). Point estimates of a 20% inhibitory concentration (IC20, i.e. the concentration of toxicant at which the response is impaired to 20% relative to the control) and corresponding 95% confidence intervals were calculated separately for each acclimation group using inverse prediction (Sokal and Rohlf 1981).

Differences in taxonomic composition of substrates were examined with Hendrickson's *M* statistic (Hendrickson 1978), which compares the number of positive matches in taxa for all pairs of substrates. Within each acclimation condition, comparisons were made stepwise, by recalculating the statistic after sequential elimination of the highest treatment groups, until heterogeneity in the number of matches in taxa was no longer significant. Concentration–response models and IC20s were calculated based on the number of pairwise matches with the similarly acclimated control. Core taxa were defined as those species present on all three replicates of a treatment. Complemented coefficients of community (Gausch 1982) were calculated for each treatment group based on core taxa and clustered using an average linkage method (SAS Institute 1985).

Overall differences in response were evaluated with multiway ANOVA, using acclimation concentration and secondary stress level as main effects and day of replication as a blocking factor. The level of secondary stress at which the outcomes for different acclimation groups converged or diverged was identified by comparison within each secondary stress level using ANOVA and Duncan's multiple range tests.

TABLE 2. Nominal and measured concentrations of Zn ($\mu g \cdot L^{-1}$).

	Nominal	Measured
Acclimation stress	Control	<25
	50	73 ± 11
	225	172 ± 34
Acute stress	Control	<25
	320	425 ± 31
	1 000	1 196 ± 96
	3 200	2 816 ± 290
	10 000	10 078 ± 1019

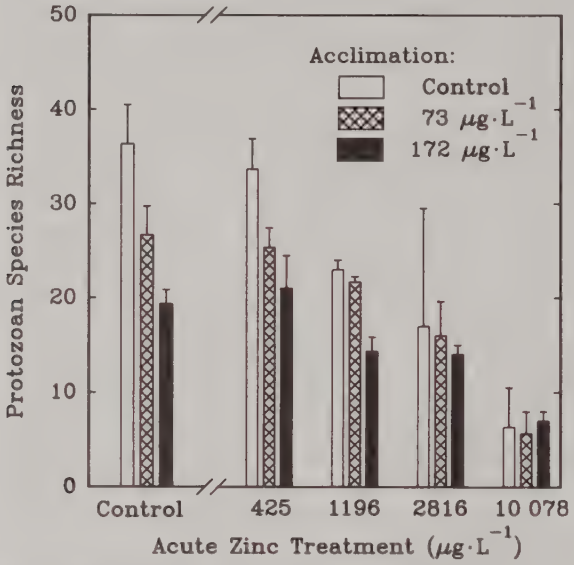

FIG. 1. Effects of secondary Zn exposure on protozoan taxonomic richness of unacclimated and Zn-acclimated communities.

Results

Measured concentrations of Zn (Table 2) indicated errors in delivered concentration from −24 to +46%. Coefficients of variation for measured concentrations within a treatment ranged from 7 to 20%. Mean measured acid-labile Zn concentrations were used for all subsequent analyses. Treatment groups are identified by measured acclimation and secondary stress levels, respectively, e.g. 73–425 refers to communities acclimated in 73 $\mu g\ Zn \cdot L^{-1}$ and secondarily exposed to 425 $\mu g\ Zn \cdot L^{-1}$.

In absence of secondary stress, unacclimated communities were taxonomically richer than acclimated communities ($p = 0.0100$; Fig. 1). With increasing secondary stress, richness declined, but acclimated communities lost fewer species relative to their initial state. This relative resistance is reflected in higher IC20 values and significantly lesser slopes ($p = 0.0007$) for acclimated communities (Table 3). The IC20 for communities acclimated in high Zn is twice that of communities acclimated without Zn. However, despite a higher IC20, acclimated communities were never taxonomically richer than unacclimated communities. After secondary exposure to ⩾2816 $\mu g \cdot L^{-1}$, differences in taxonomic richness between acclimation groups were no longer significant ($p \geqslant 0.800$). The taxonomic richness of acclimation groups converged with cumulative stress.

TABLE 3. Biologically significant levels of Zn ($\mu g \cdot L^{-1}$) for taxonomic richness of communities acclimated to Zn.

	Acclimation concentration		
Response	Control	73	172
LOEC	1196	1196	1196
IC20	696	992	1420
95% confidence interval	178–1711	530–1641	663–2873
r^2	0.757	0.933	0.848
Intercept	84.43	65.31	45.46
Slope	−8.51	−6.41	−4.14
Standard error of slope	1.52	0.57	0.55
p-value for regression	0.0002	0.0001	0.0001
p-value for lack-of-fit	0.9386	0.2350	0.1870

TABLE 4. Biologically significant levels of Zn ($\mu g \cdot L^{-1}$) for taxonomic composition of communities acclimated to Zn.

	Acclimation concentration		
Response	Control	73	172
LOEC	2816	2816	1196
IC20	1172	1086	1693
95% confidence interval	329–3748	403–2774	477–5866
r^2	0.647	0.740	0.623
Intercept	40.08	32.46	23.38
Slope	−3.861	−3.116	−1.997
Standard error of slope	0.4894	0.3164	0.2665
p-value for regression	<0.0001	<0.0001	<0.0001
p-value for lack-of-fit	0.2849	0.0012	0.2377

Despite significant differences in taxonomic richness, differences in composition of acclimated communities in absence of secondary stress were not significant ($p = 0.1485$). Mean number of taxa in common was 16.0 ± 1 within control–control (C–C) communities and 13.4 ± 2.5 and 11.4 ± 1.7 between C–C and low and high Zn acclimations, 73–C and 172–C, respectively. Increasing levels of secondary stress resulted in progressive dissimilarity from initial community composition (Table 4). Taxonomic composition of acclimated communities changed less in response to secondary stress than controls. The slopes of the concentration–effect models differed significantly ($p = 0.0062$). The cluster pattern shows initial separation between acclimation groups followed by greater persistence of similarity within acclimated communities after a subsequent stress (Fig. 2).

Several core taxa (*Cinetochilum margaritaceum* and *Microthorax bidendatus*) were important only in control communities never exposed to Zn (Table 5). Other taxa were unimportant in absence of Zn but persisted through high acute Zn concentrations in acclimated communities (*Aspidisca costata* and *Bodo uncinatus*) and/or were important only in the presence of Zn (*Trachelophyllum pusillum* and *Carteria* sp.).

Neither AFDW nor IVF distinquished acclimation groups in absence of secondary stress ($p = 0.1519$ and 0.9715, respectively). Secondary stress had no significant effect on either measure ($p = 0.9035$ and 0.3317, AFDW and IVF, respectively). Mean total biomass ranged from 129 ± 58 mg

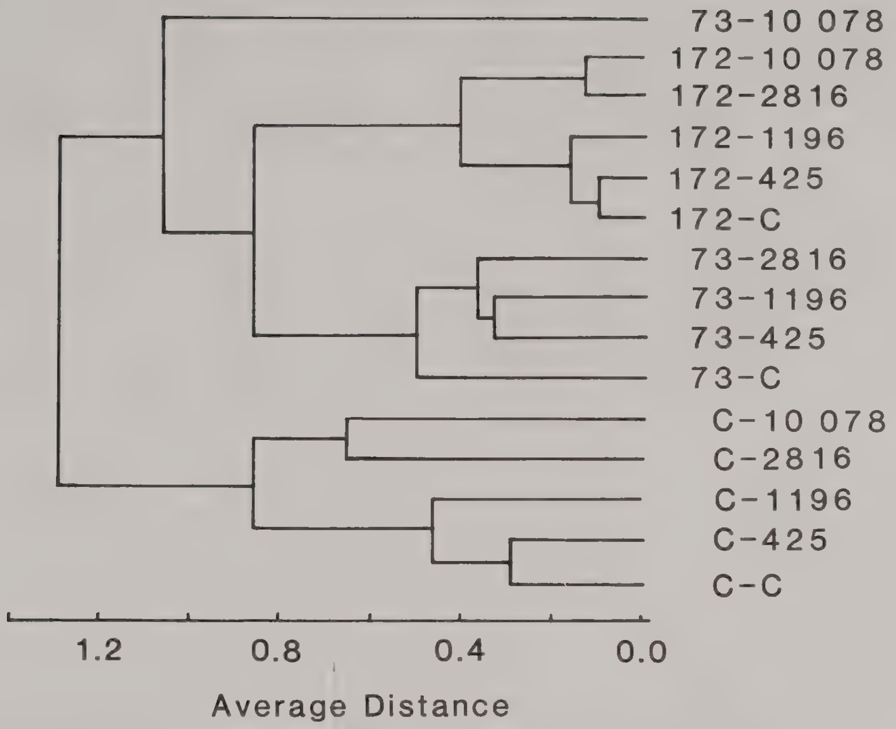

FIG. 2. Similarity in taxonomic composition of unacclimated and Zn-acclimated communities subjected to secondary Zn stress.

TABLE 5. Patterns of occurrence of core protozoan taxa across increasing secondary stress levels.

	Acclimation stress level														
Taxon	C					73					172				
Ciliates															
Aspidisca costata	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0
Cinetochilum margaritaceum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colpoda aspera	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ctedoctema acanthocrypta	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cyclidium sp.	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0
Glaucoma sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Litonotus faciola	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Mesodinium acarus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Microthorax bidentatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachelophyllum pusillum	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Vorticella campanula	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sarcodines															
Cochliopodium sp.	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0
Heterotrophic flagellates															
Bodo uncinatus	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1
Cyathomonas truncatum	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1
Entosiphon sulcatum	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
Monas sp.	1	1	1	1	0	0	1	1	1	0	0	1	1	0	0
Monosiga sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Peranema trichophorum	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Petalomonas sp.	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0
Photosynthetic flagellates															
Carteria sp.	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0
Chlamydamonas sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cryptomonas erosa	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0

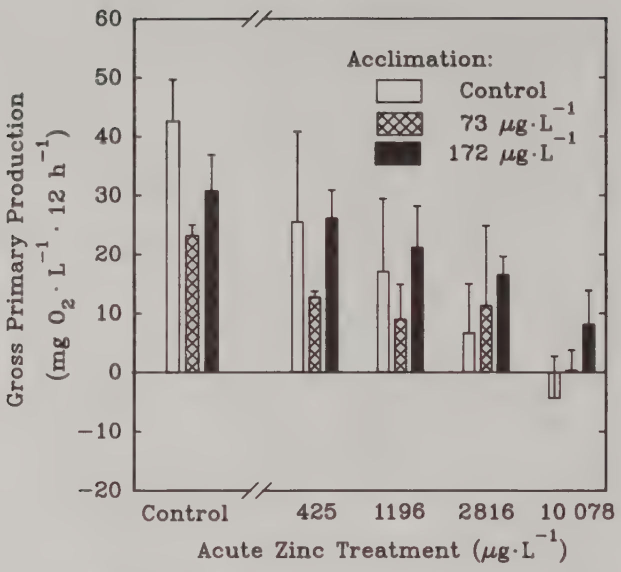

FIG. 3. Effects of secondary Zn exposure on gross primary productivity of unacclimated and Zn-acclimated communities.

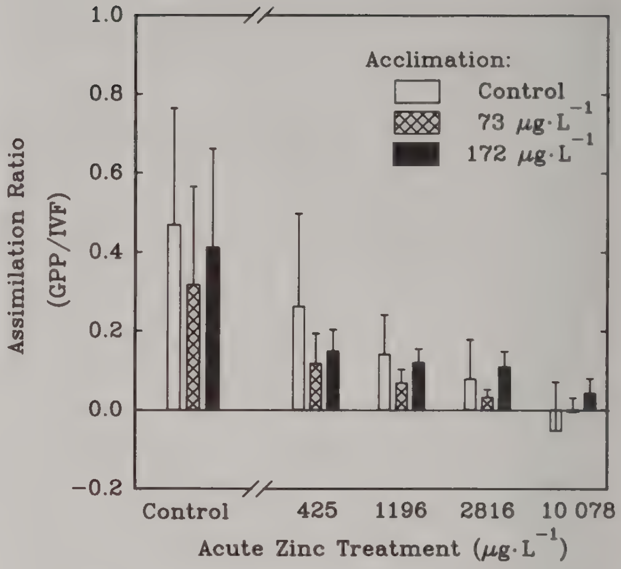

FIG. 4. Effects of secondary Zn exposure on assimilation ratio of unacclimated and Zn-acclimated communities.

TABLE 6. Biologically significant levels of Zn (μg·L^{-1}) for gross primary production of communities acclimated to Zn.

	Acclimation concentration		
Response	Control	73	172
LOEC	425	425	1196
IC20	180	87	605
95% confidence interval	3–774	2–365	103–1830
r^2	0.594	0.699	0.689
Intercept	9.679	4.222	7.021
Slope	−1.107	−0.461	−0.654
Standard error of slope	0.2893	0.1009	0.1389
p-value for regression	0.0033	0.0014	0.0008
p-value for lack-of-fit	0.9697	0.8498	0.9436

TABLE 7. Biologically significant levels of Zn (μg·L^{-1}) for assimilation ratio of communities acclimated to Zn.

	Acclimation concentration		
Response	Control	73	172
LOEC	10 078	>10 078	2816
IC20	123	10	1
95% confidence interval	<1–890	<1–51	<1–29
r^2	0.457	0.581	0.517
Intercept	0.0705	0.0288	0.0285
Slope	−0.0081	−0.0032	−0.0026
Standard error of slope	0.0028	0.0009	0.0008
p-value for regression	0.0158	0.0064	0.0084
p-value for lack-of-fit	0.9823	0.9414	0.7609

AFDW·L^{-1} in C–C communities to 54 ± 12 mg AFDW·L^{-1} in the 72–10 078 treatment. Mean IVF ranged from 187 ± 49 FU in the 172–425 treatment to 61 ± 30 FU in the C–10 078 group.

In absence of secondary stress, GPP was not significantly different between acclimation groups ($p = 0.0556$). Secondary stress reduced GPP ($p = 0.0001$), but decreases were less pronounced in Zn-acclimated groups ($p = 0.0078$) (Fig. 3; Table 6). After secondary exposure to 10 078 μg·L^{-1}, GPP in communities acclimated to 172 μg Zn·L^{-1}, was significantly higher than that in other acclimation groups ($p = 0.0153$). IC20 values more than tripled from 180 μg·L^{-1} for the control to 605 μg·L^{-1} for the group acclimated to 172 μg Zn·L^{-1}.

Effects on AR were similar to those for GPP (Fig. 4). Weighting production rate by algal biomass reduced differences between acclimation groups but did not change overall patterns of response across secondary stress, suggesting that the integrity of photosynthetic function was affected. Initial differences between acclimation groups in absence of secondary stress were not significant ($p = 0.0649$). Slopes of concentration–effect models decreased with increasing acclimation stress ($p = 0.0077$) (Table 7). The IC20 for unacclimated communities was higher than those for acclimated communities, but all IC20s were extrapolated below the lowest tested concentration. Unlike GPP, AR was never significantly higher in acclimated communities than in unacclimated communities ($p \geqslant 0.1957$).

Respiration rates were quite variable. Acclimation groups did not differ in CR in absence of secondary stress ($p = 0.2766$), and secondary stress had no significant effect ($p = 0.6369$). Mean CR ranged from 4.09 mg O_2·L^{-1}·24 h^{-1} in 73–10 078 and 172–10 078 communities (standard deviations were 2.69 and 9.56, respectively) to 23.73 ± 24.69 mg O_2·L^{-1}·24 h^{-1} in the C–2816 group.

Similarly, respiration to biomass ratios were quite variable and did not differ significantly either initially ($p = 0.5750$) or in response to subsequent stress ($p = 0.7569$). Mean respiration to biomass ratios ranged from 0.00239 ± 0.0040 mg O_2·24 h^{-1}·mg AFDW^{-1} in 172–10 078 to 0.0119 ± 0.0133 mg O_2·24 h^{-1}·mg AFDW^{-1} in C–2816.

TABLE 8. Biologically significant levels of Zn (µg·L^{-1}) for net daily metabolism of communities acclimated to Zn.

	Acclimation concentration		
Response	Control	73	172
LOEC	2816	425	2816
IC20	172	34	501
95% confidence interval	<1–1097	<1–268	34–1920
r^2	0.454	0.557	0.598
Intercept	63.98	27.42	34.53
Slope	−9.412	−3.573	−3.392
Standard error of slope	3.266	1.063	0.8789
p-value for regression	0.0163	0.0083	0.0032
p-value for lack-of-fit	0.6589	0.3163	0.4846

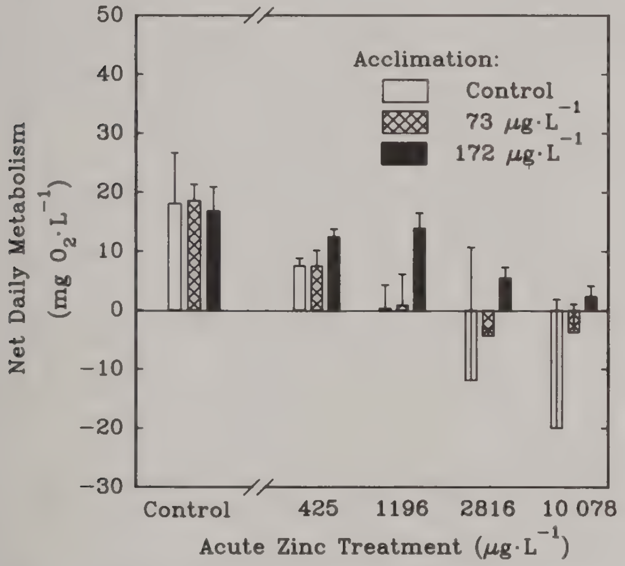

FIG. 5. Effects of secondary Zn exposure on net daily metabolism of unacclimated and Zn-acclimated communities.

In the absence of secondary stress, NDM was similar for all acclimation groups (p = 0.8500). It declined in response to secondary stress (p = 0.0001) (Fig. 5) but was affected less in acclimated communities than in the control. The slopes of the concentration–effect model were significantly different (p = 0.0095) (Table 8). IC20 values nearly tripled from 172 to 501 µg·L^{-1}.

In the absence of secondary stress, ratios of soluble to total phosphates were not significantly different between acclimation groups (p = 0.1672). Secondary stress had no significant effect (p = 0.0629). Mean values ranged from 0.23 ± 0.03 in C–2816 to 0.02 ± 0.01 in 172–425.

Discussion

Aufwuchs communities developed under different levels of Zn stress responded differently to subsequent Zn stress. Differences were significant for taxonomic richness and composition and for a suite of measures incorporating primary production (i.e. GPP, AR, and NDM). In general, communities developed under Zn stress were initially impaired but changed less in response to additional stress relative to their initial state. Relative resistance, expressed as IC20s, increased up to a factor of 3.4 with acclimation. Absolute outcome for different acclimation histories converged with increasing secondary stress. At high levels of secondary stress, no significant differences emerged between acclimated groups in taxonomic richness, composition, AR, or NDM. However, GPP was significantly less impaired in communities acclimated in 172 µg Zn·L^{-1} than in controls after secondary exposure to 10 078 µg Zn·L^{-1}, providing some evidence for an absolute increase in tolerance. This tolerance increase occurred at Zn levels that had clearly unacceptable effects on the biological integrity of the community (e.g. at this level, <10 taxa remained and GPP was ≤30% of initial levels). There was no response monitored for which acclimated communities showed significant decreases in tolerance relative to the control.

The increases in relative tolerance observed in this study (3.4 ×) were in the same range as those reported for fish acclimated to Zn (2–5 ×; Chapman 1985). In community-level experiments (DeNoyelles and Kettle 1985; DeNoyelles et al. 1989), primary production of phytoplankton communities in experimental ponds treated with atrazine rapidly recovered to control levels. Subsequent exposure to an additional 100 µg atrazine·L^{-1} decreased ^{14}C uptake ≤20% in phytoplankton communities from ponds acclimated to 100 µg·L^{-1}, but unacclimated communities showed decreases from 40 to 80%. In this study, exposure to 425 µg Zn·L^{-1} decreased GPP 15% in communities acclimated to 172 µg Zn·L^{-1}, but unacclimated communities showed decreases of 40%. Blanck and Wängberg (1988) found that IC20s for primary productivity changed by ≥1000 × with acclimation to arsenate compared with our maximum differences of 3.4 ×. Two factors may contribute to this difference. Blanck and Wängberg (1988) tested communities acclimated over a broader range of arsenate concentrations (0.1–10 µM) than our Zn concentrations (6.5–154 µM). They also suggested that tolerance is best detected by monitoring an endpoint closely related to the mode of action of the toxicant.

To put our range of Zn concentrations in perspective, acclimation levels (73 and 172 µg·L^{-1}) were above background concentrations (≤10 µg·L^{-1}; Inhat 1981) and above the chronic criterion (47 µg·L^{-1}) for protection of aquatic life in the United States (U.S. Environmental Protection Agency (USEPA) 1980). However, acclimation levels are still in the range found in some surface waters in the United States (LaPoint et al. 1984). Secondary stress levels in this study ranged from 425 to 10 078 µg·L^{-1}, which exceed the acute criterion for protection of aquatic life (250 µg·L^{-1} at a hardness of 74 mg·L^{-1}; USEPA 1980) but are within the range reported in damaged natural systems (LaPoint et al. 1984). Reports of acutely toxic concentrations of Zn range from 90 µg·L^{-1} for fish in the genus *Salmo* to 58 100 µg·L^{-1} for an unidentified caddisfly (USEPA 1980). The twentieth percentile for mean acute values for all genera tested was 1207 µg·L^{-1}. This value can be compared with the IC20s for taxonomic richness in this study (696, 992, and 1420 µg·L^{-1}). The Zn concentrations used in this study were within the range of toxic stress occurring in surface waters, and the response of the *aufwuchs* communities to stress seems consistent with other observations of Zn toxicity.

The management implications of increases in tolerance resulting from previous stress exposure are debated. The concept of pollution-induced community tolerance (PICT) defines increased tolerance as evidence of species selection and structural impairment (Blank and Wängberg 1988). However, increased tolerance can also be viewed as evidence of ecosystem resilience and/or repair, which may increase the concentration of chemical required to cause a specified unacceptable biological impairment (e.g. Stockner and Antia 1976). If increased tolerance is viewed as potentially protective, comparison of IC20 values to evaluate environmental outcome can be misleading when there are initial differences in acclimated and unacclimated groups. If the IC20 value is higher, relative tolerance has increased and the community will be less changed by subsequent stress, but comparisons with unimpaired communities must be made to evaluate net impairment. Despite higher IC20 values, acclimated communities in this study were never more taxonomically rich than controls. The higher IC20 value did not translate into greater species richness, so acclimation seemed to provide no net protection from the effects of subsequent stress. DeNoyelles et al. (1989) also made this distinction between relative tolerance and net impairment in their study of phytoplankton communities exposed to atrazine in artificial ponds. Because there were no initial differences in ^{14}C uptake, the differences between acclimation groups in subsequent response reflected differences in net impairment. So, they stated ". . . tolerance is clearly indicated, and not merely a community of already inhibited organisms showing less further inhibition to an addition of more of the same toxicant."

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Factors Affecting the Vulnerability of Juvenile Coho (*Oncorhynchus kisutch*) and Chinook Salmon (*O. tshawytscha*) in a Saltwater Sport Fishery

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Holtby, L. B., R. K. Kadowaki, and K. S. Simpson. 1992. Factors affecting the vulnerability of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) in a saltwater sport fishery. Can. J. Fish. Aquat. Sci. 49: 2164–2178.

The fork length, origin (hatchery or wild), and sex and age composition of sport- and seine-caught juvenile (no sea winter annulus) coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) were compared in Saanich Inlet, British Columbia. Sport-caught coho and chinook were larger and had a higher proportion of males than seine-caught fish. The sport fishery was strongly size- selective for both species, resulting in the overrepresentation of jack coho and freshwater age 1 juvenile chinook in the sport catch. Marked coho and chinook were overrepresented in the sport catch, indicating that hatchery fish were more vulnerable to the sport fishery than wild fish. For both species, the higher vulnerability of hatchery fish to the sport fishery could not be fully explained on the basis of size, sex, or freshwater age. Relative to older fish, juvenile coho and chinook were more vulnerable to fishing methods that used light gear at shallow depths (< 30 m), such as trolling and casting. Assumptions by managers that vulnerability of coho and chinook does not vary with size, sex, freshwater age, or origin need to be reexamined in light of these findings.

On a comparé dans l'inlet Saanich (Colombie-Britannique) la longueur à la fourche, l'origine (poissons d'élevage ou sauvages) et la répartition par sexe et par âge des juvéniles (pas d'anneau de croissance d'hiver en mer) chez des saumons cohos (*Oncorhynchus kisutch*) et quinnats (*O. tshawytscha*) capturés à la pêche sportive et à la senne. Les poissons des deux espèces capturés à la pêche sportive étaient plus grands et présentaient une plus forte proportion de mâles que les poissons pris à la senne. La pêche sportive était fortement sélective en ce qui concerne la taille chez les deux espèces, ce qui causait une surreprésentation des "jacks" chez les cohos et des jeunes quinnats d'eau douce âgés d'un an dans les prises sportives. Les cohos et les quinnats marqués étaient surreprésentés dans les prises sportives, ce qui indique que les poissons d'élevage étaient plus vulnérables à la pêche sportive que les poissons sauvages. Chez les deux espèces, la plus forte vulnérabilité des poissons d'élevage à la pêche sportive ne pouvait s'expliquer pleinement en fonction de la taille, du sexe, ou de l'âge en eau douce. Par rapport aux poissons plus âgés, les juvéniles cohos et quinnats étaient plus vulnérables aux méthodes de pêche qui faisaient appel à des agrès légers à faible profondeur (< 30 m) comme la pêche à la traîne et au lancer. Il serait bon de réexaminer à la lumière de ces résultats l'opinion admise parmi les gestionnaires selon laquelle la vulnérabilité du coho et du quinnat ne varierait pas avec la taille, le sexe, l'âge en eau douce ni l'origine.

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Ocean sport fisheries for Pacific salmon (*Oncorhynchus* spp.) concentrate on two species: coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*). In sport fisheries within the Strait of Georgia, most fish of legal size are retained by anglers and are subsequently sampled for species, length, and age (English et al. 1986). Anglers are also encouraged to turn in heads containing coded wire tags (CWTs) that, along with biological information from the fish, provide stock-specific information on size and distribution. Consequently, the magnitude and dynamics of the sport fishery, as well as the biological characteristics of the catch, with the exception of stock composition, are fairly well known.

The retention of coho less than 30 cm and chinook salmon less than 62 cm (45 cm at the time of this study) is prohibited, but it is known that many juvenile salmon (fish in their first summer in the ocean) are caught and released alive. Up to 1 million juvenile coho and chinook are released alive in the Strait of Georgia, a total that is similar to the number of fish legally retained (Shardlow and Collicutt 1989a, 1989b). Estimates of the mortality suffered by released fish varies widely; values of between 20 and 30% are typical (Wright 1970; Wertheimer 1988). Recent work suggests that mortalities of 15% for coho and 40% for chinook are more typical of sport-caught salmon less than 30 cm fork length (T. Gjernes, Pacific Biological Station, Nanaimo, B.C., pers. comm.). Consequently, shaker mortality is probably an important component of the total fishing mortality suffered by these species.

The lands around the Strait of Georgia are undergoing rapid urbanization with consequent increases in ocean sport fisheries within the Strait. Increased fishing pressure requires more intense management which entails not only more extensive knowledge of the life histories of target species but also more detailed information on the nature of the fishery. Management actions designed to reduce juvenile mortality, although potentially very beneficial, are hindered by a lack of knowledge of the characteristics of released fish of sublegal size (Argue et al.

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[1] The order of the authors is alphabetical.

1983). Of particular concern is the extensive use of hatchery stocks as indicators of survival and harvest pattern for wild stocks.

In this study we compare the characteristics of sport-caught chinook and coho salmon juveniles with contemporaneous samples taken with small-mesh seine gear. Our objective was to examine the effects of sportfishing gear, size, sex, and origin on the vulnerability of juvenile coho and chinook during their first summer and fall of ocean residency. All of the data presented in this paper are summarized from the complete listing available in Simpson and Kadowaki (1992).

Study Species and Area

In southern British Columbia, wild coho salmon enter the ocean during the spring (March through June) after spending 1 or 2 yr in freshwater. Many males and all females remain in the ocean for 18 mo (rarely 30 mo) before returning to spawn and die in the fall and winter (September through February). Some males (jacks) return to freshwater to spawn after 6 mo in the ocean. Fish are taken by ocean sport fisheries as early as 3 mo after ocean entry but, in most jurisdictions, do not attain sufficient size to be legally retained until 8–10 mo after ocean entry. Coho originating from hatcheries constitute approximately 50% of the fish taken by sport fisheries in the Strait of Georgia (Farlinger et al. 1990). Hatchery smolts are released at times similar to the migration times of wild smolts. Hatchery smolts are generally larger than wild smolts, and all have been reared for 1 yr in freshwater. In Canadian and American hatcheries, 5–15% of production is routinely tagged and marked, usually with CWTs and an adipose clip. In 1985, the year of our study, 80–90% of the coho released from Strait of Georgia hatcheries were either marked with a pelvic fin clip or tagged with CWTs and adipose clipped. (Fish with either fin clips or CWTs are collectively referred to as marked fish.)

The life history of chinook salmon is more variable than that of coho. Most wild chinook smolts enter the ocean in early summer after spending 3 mo in freshwater (90-d smolts), but significant numbers either enter the ocean soon after emergence in the spring or remain in freshwater for 1 yr. The differences in the timing of ocean entry are probably genetically based (Carl and Healey 1984). Individuals remain in the ocean for 18–54 mo (typically 30 or 42 mo). Chinook generally attain sufficient size to be retained in the sport fishery by their third summer of ocean life. Chinook produced in hatcheries are usually developmentally accelerated and are released in the spring at sizes similar to 90-d wild smolts. Approximately 10–18% of chinook salmon taken in the Strait of Georgia sport fishery are from Canadian hatcheries and approximately 10–15% of Canadian production is tagged with CWTs. Chinook from American hatcheries make up approximately 25% of the sport catch in the Strait of Georgia (P. Starr, Pacific Biological Station, Nanaimo, B.C., pers. comm.). Approximately 5% of American production is tagged.

Saanich Inlet is located on the southeast corner of Vancouver Island, north of the city of Victoria (Fig. 1). The inlet is a popular location for sport fishing and provided a relatively confined area where we could safely seine for juvenile salmon. The inlet is sufficiently well sheltered that sport fishing is seldom disrupted by inclement weather. Most of the sport fishermen launched from a single site, simplifying the tasks of interviewing and catch sampling.

Methods

Seine Sampling

We captured juvenile chinook and coho with seine gear during four sampling periods covering a total of 37 d in the summer and fall of 1985. The sampling periods correspond approximately to the months of July through October. We used two vessels: a 17-m seiner of 37.5 t for the first and third periods and an 11-m seiner of 9.3 t for the other two periods. The seine net of the first vessel was 275 m long by 26 m deep with the size of the mesh graduated from 51 mm in the lead to 10 mm in the bunt. The seine net on the second vessel was 210 m long by 22 m deep with the size of the mesh graduated from 51 mm in the lead to 6 mm in the bunt. The effective fishing depth of each seine net was approximately 2 m less than its maximum depth.

We began fishing each day at about 07:30. We usually stopped fishing by midafternoon, but occasionally fished later when catches were poor (<100 fish). At the start of each sampling series, we fished throughout Saanich Inlet, including areas where there appeared to be concentrations of sport fishermen. Average catches were consistently much higher along the west shore of the inlet between Mill Bay and McCurdy Pt., and we concentrated fishing there toward the end of each sampling period. We made one to 10 (usually six or seven) sets each day. Catches ranged from 0 to 108 juvenile coho$\cdot$set^{-1} (median 6) and from 0 to 47 juvenile chinook$\cdot$set^{-1} (median 2). In many sets, no juvenile salmonids were captured.

We enumerated the catches of all fish species. We visually estimated large catches of Pacific herring (*Clupea pallasi*) and Pacific sand lance (*Ammodytes hexapterus*). Coho and chinook were killed in a tub with carbon dioxide, immediately refrigerated, and sampled at the end of the day. Twice, we froze catches and sampled them the next day. We recorded the fork length (to the nearest millimetre), sex, and presence of fin clips. We determined sex by visually examining the gonads. Coho jacks, although recognizable in period 1, were not recorded separately from nonmaturing males until period 2. However, the size distribution of male coho in period 1 was moderately skewed right and was bimodal with approximately 5% of the males in the upper mode and right tail of the distribution, a proportion similar to the nearly constant proportion of maturing males caught in periods 2 and 3 (Table 1). Since the largest males caught in periods 2 and 3 were usually jacks, we reclassified the largest 5.8% (the average proportion in periods 2 and 3) of males in period 1 as jacks. We took two to five scales for aging and kept heads from fish with missing adipose fins for extraction and decoding of CWTs.

Sport Sampling

We interviewed sport fishermen and sampled their catches at the Tsartlip boat launching ramp (Fig. 1) from dawn to dusk on 43 d between early July and the end of November 1985. For comparison with the seine samples, the sport sample dates were assigned to the closest seine sampling period. As they were preparing to launch their boats, we gave fishermen an information bulletin on the program and asked if they would like to participate. Fishermen who agreed to participate were given an individually numbered permit that authorized them to retain sublegal coho and chinook for that day, labels for each fish, on which the anglers were to record how, when, and where the fish had been caught, and an instruction sheet. We asked participants to note the size and species of any salmon that they

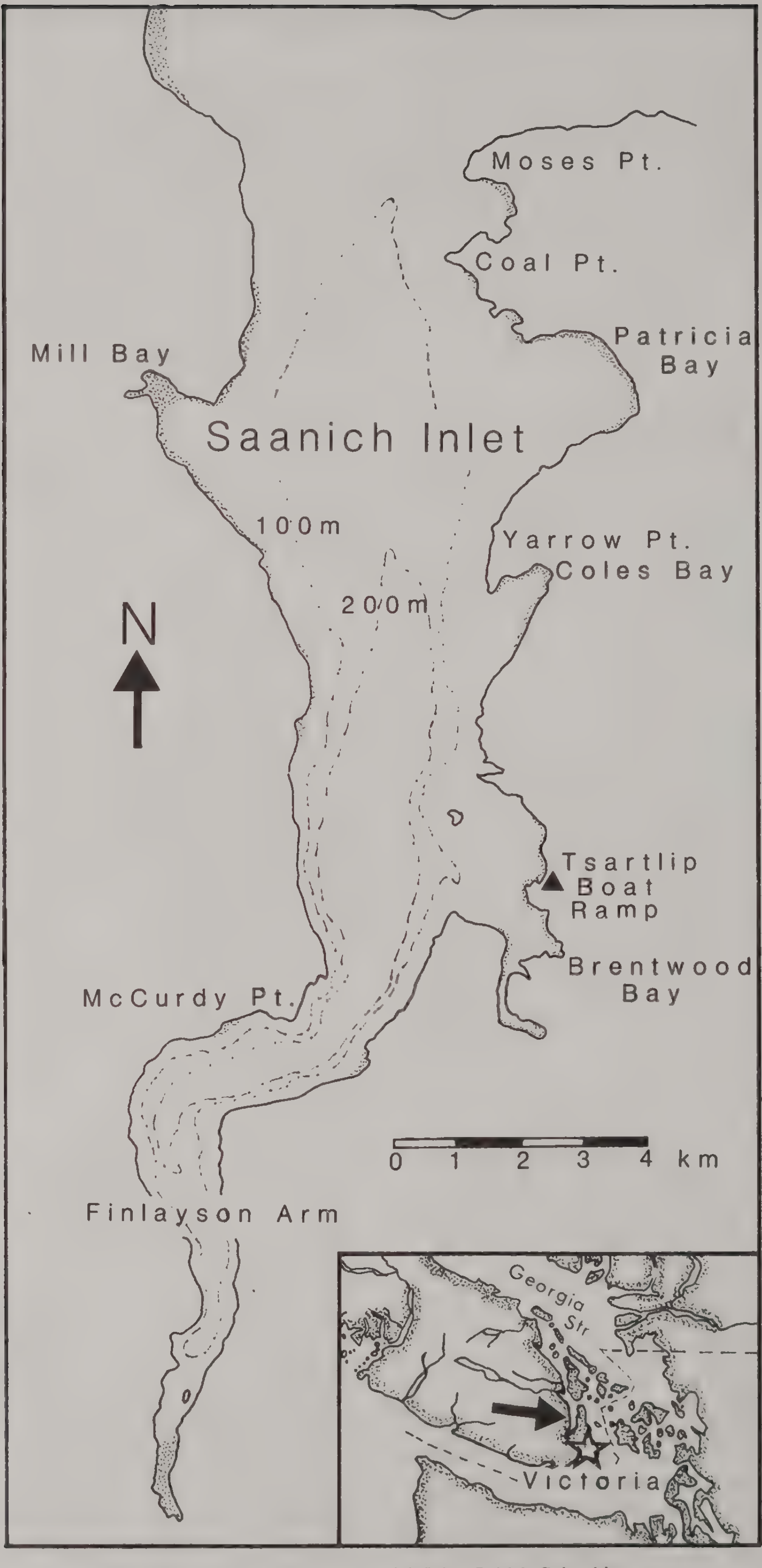
Moses Pt.
Coal Pt.
Patricia Bay
Mill Bay
Saanich Inlet
100m
Yarrow Pt.
Coles Bay
200m
N
Tsartlip Boat Ramp
Brentwood Bay
McCurdy Pt.
0 1 2 3 4 km
Finlayson Arm
Georgia Str
Victoria

FIG. 1. Map of study area, Saanich Inlet, British Columbia.

TABLE 1. Numbers of juvenile coho sampled and proportions of male (p_{males}), maturing male (p_{maturing}), marked (p_{marked}), and freshwater age 1. (p_1) juvenile coho in the seine and sport catches by period. *$P < 0.05$, **$P < 0.005$ H_0: proportions in seine and sport catches are equal (G-test).

Sampling period	n_{seine}	n_{sport}	p_{males}		p_{maturing}		p_{marked}		p_1	
			Seine	Sport	Seine	Sport	Seine	Sport	Seine	Sport
1	1095	25	0.520	0.680*	—	—	0.050	0.080	0.989	1.0
2	940	147	0.478	0.558*	0.051	0.159**	0.062	0.116**	0.981	0.982
3	968	138	0.485	0.558	0.064	0.052	0.061	0.109*	0.974	0.935
4	114	21	0.500	0.667	0.0	0.0	0.132	0.095	0.949	1.0
Overall	3117	331	0.504	0.584**	0.057	0.098*	0.058	0.109**	0.982	0.965

chose to release. When we interviewed the fishermen at the end of their trip, many recalled the unrecorded details of how and when released salmon were caught. We know that some fish caught and released were not reported and assume that nonreporting was random with respect to size and mark incidence.

We asked fishermen returning to the ramp to turn in their questionnaires, permits, and any sublegal fish that they had retained. We recorded the time of sampling, species, sex, fork length (to the nearest millimetre), and the presence and type of fin clips of all fish caught. We preserved all sublegal fish in formalin for later resampling in the laboratory, where the maturation state of males was determined. We took the heads of legal fish with missing adipose fins for later extraction of CWTs. Two to five scales were taken for age determination.

We also recorded the angling method used in capturing each fish. The sport fishermen we interviewed used a variety of methods and gear types. The important differences between the methods involved the depth of fishing and how the gear was moved through the water vertically and horizontally (''played''). Most fishermen used one of three variants of trolling. In all forms of trolling, weighted gear is towed behind a boat. Trolling with a lead sinker was the simplest variant. Simple troll gear does not usually fish deeper than 10 m (T. Gjernes, Pacific Biological Station, pers. comm.). The second type of trolling uses a planer, a wing-like device attached to the fishing line ahead of the lure, to sink the lure deeper than can be achieved with lead sinkers alone. The depth that a planer can achieve is positively correlated with its weight, with the amount of line put out, and with the speed at which it is trolled, but is typically less than 20 m. It is possible to fish deeper, but the weight and heavy line required are seldom used (T. Gjernes, Pacific Biological Station, pers. comm.). Estimation of the actual fishing depth while trolling or planing is difficult because of the angle of the line, the great lengths of line that are often used, and unseen curvatures of the line underwater. The third variant of trolling uses a downrigger consisting of a large lead ball suspended by a cable. The fishing line is attached to the cable near the ball by a device that releases the line when a fish strikes the lure. Downriggers usually have an indicator for the amount of line out and the heavy weight on the line holds it nearly vertical, so estimated fishing depths with this gear should be accurate. However, the heavy weights used with downriggers make it difficult to detect small fish, which often strike the lure while the gear is being raised or lowered.

The three other methods observed were used from stationary or drifting boats. In jigging, a weighted lure is sunk to the desired depth, usually just off the bottom, and then played vertically by repeatedly lifting and lowering the rod. In casting, a weighted lure is cast from the rod, sunk (usually to a shallow depth), and reeled in. Often the line is jigged while being reeled in. In mooching, bait (generally herring) with hook(s) attached is sunk to a specific depth, often just off the bottom. Mooching allows the greatest control of both fishing depth and location. For all three methods the nearly vertical hang of the line should have enabled accurate estimation of fishing depth.

Effects of Delayed Sampling on Length Measurements

We seldom sampled sport- or seine-caught salmon immediately after capture. The average delay in sampling sport catches was about 3 h and the average delay for seine catches was about 6 h. Such delays could have affected measured fork lengths. Sport catches were more likely to have been affected because most fishermen did not refrigerate their catches. To estimate the effects of delayed sampling on fork length measurements of unrefrigerated fish, we did not refrigerate 65 coho caught in the six seine sets of July 8. We measured and labeled each fish immediately after death and remeasured them as many as four times through the course of the day. Between measurements, the fish were covered and kept on deck out of the sunlight. Similar practices were followed by most sport fishermen.

Age Notation

Ages are denoted following the European system of Koo (1962) in which the number of winters spent in freshwater and the ocean are given. For example, most of the juvenile coho sampled were aged 1.0, having reared over one winter in freshwater and having been captured in their first summer in the ocean.

Size–Time Trajectories

Two models were used to describe the size–time trajectories of sampled fish. For all chinook groups and for maturing coho salmon males, a simple exponential model

$$(1)\quad \log_e \mathrm{FL}_t = a + Kt$$

was suitable, where FL_t was the fork length on the day of sampling and t was the day of the year of sampling. The parameters K and a were estimated with simple linear regression. For the remaining coho groups the Pütter (von Bertalanffy) growth equation (Ricker 1975)

$$(2)\quad \mathrm{FL}_t = L_\infty(1 - \exp(-K(t - t_0)))$$

was fitted to fork length – time data with the nonlinear parameter estimator of SYSTAT (Wilkinson 1988). Confidence intervals for the parameter estimates (L_∞, K, and t_0) were calculated with the Hessian estimation procedure of the SYSTAT NONLIN module.

Selectivity of Sport Gear

In determining the selectivity of sport gear for size, sex, freshwater age, and origin, we have assumed that the seine samples were unbiased samples of the inlet populations. To estimate size selectivity, we first generated size–frequency distributions of the seine and sport catches with 1-cm size classes. If class totals in the seine catch were less than five, adjacent classes were combined, summing toward the modal class. The same classes were summed in the sport catch. If sport-caught fish were of a size not caught in the seine, then the sport-caught class was combined with the nearest class, again summing toward the modal class. Selectivity was then calculated by dividing the sport size–frequency distribution by the seine distribution and plotting the ratios against the midpoints of the size classes. Because we had no theoretical basis for selecting any particular model (Regier and Robson 1966), we plotted Distance Weighted Least Squares (DWLS) lines (McLain 1974) through the points to reveal the general nature of the size-selectivity curves. An absence of size selectivity would be indicated by a flat line (i.e. a constant ratio) with a value equal to the ratio of the total sport catch divided by the total seine catch. To estimate the selectivities of sport gear for sex, freshwater age, and origin, we compared the categorized sport and seine catches with the G or log-likelihood ratio test (Zar 1974):

$$(3) \quad G = 2 \sum f_i \ln f_i / F_i$$

where f_i is the observed frequency in the ith of k classes and F_i is the frequency in the seine catch or the expected frequency. The distribution of G approximates the χ^2 with $k - 1$ degrees of freedom.

To compare the average size of juvenile fish caught between the various sport methods, we first estimated, by day, species, and sex, the average size of fish in the inlet populations with the appropriate growth equation (see above) with parameter values estimated from the seine catch (see below). After calculating the differences between the fork length of each sport-caught fish and the average of seine-caught fish on that day, variation in fork length between sport methods was examined with ANOVA and post hoc comparisons.

To estimate the relative vulnerabilities of distinct groups (e.g. marked and unmarked fish) of juvenile fish in the sport fishery, we calculated the ratio of exploitation rates on the two groups. For example, assume that of 1000 fish captured by seine, 900 were of type A ($N_A^{\text{seine}} = 900$) and 100 were of type B ($N_B^{\text{seine}} = 100$). Assume that of 100 fish caught in the sport fishery, 50 were of type A ($N_A^{\text{sport}} = 50$) and 50 were of type B ($N_B^{\text{sport}} = 50$). The exploitation rate on fish of type A in the sport fishery is

$$E_A = N_A^{\text{sport}} / N_A^{\text{seine}} = 0.056,$$

while the exploitation rate on group B is

$$E_B = N_B^{\text{sport}} / N_B^{\text{seine}} = 0.5.$$

The ratio of the exploitation rates, $E_B / E_A = 8.9$, indicates that a type B fish is 8.9 times more likely to be caught than a type A fish or, alternatively, that the sport fishery is removing fish of type B 8.9 times faster than fish of type A. Strictly speaking, E_A and E_B are not exploitation rates, since we know neither the magnitude of the sport catch nor size of the exploited populations. However, assuming that the seine samples are unbiased for whatever attribute characterizes the two groups, E_A and E_B are proportional to the actual exploitation rates.

Results

Effects of Delayed Sampling on Length Measurements

Fish kept in the shade on the deck of the seine boat quickly shrank, presumably due to rigor mortis. Most of the shrinkage had already occurred after 45 min, the time of the earliest remeasurement. The mean length after delays of 0.75–2.6 h was 98.3% (SE = 0.14) of the initial length. Fork lengths had returned to their initial values 2.6–3.3 h after death. The mean relative length for remeasurements taken 3.3–9.1 h after death was 100.0% (SE = 0.12) of the initial size.

We expect similar effects for the refrigerated seine catch. Halliday and Roscoe (1969) concluded from their own measurements of iced Atlantic cod (*Gadus morhua*) and Atlantic argentine (*Argentina silus*) and from four other studies that changes in length are often less than 1%. Since delays of between 3 and 6 h between death and sampling were typical in our study, we concluded that no corrections to measured fork lengths were required.

Characteristics of Resident Fish as Revealed by Seine Sampling

We caught 3117 juvenile coho over the four sampling periods. Catches were lower in the last sampling period, despite increased effort (Simpson and Kadowaki 1992), and we suspect that numbers of juvenile coho and chinook salmon declined in October.

The proportion of male coho in the seine catch varied from 0.478 to 0.520 (Table 1) with no discernible temporal trend. None of the observed values differed significantly from 0.5 or from each other. Maturing males were seen in period 1 but were not recorded until period 2. In the second and third periods, 5.1 and 6.4%, respectively, of males were maturing (Table 1). In the fourth period, no maturing males were found and we suspect that the jacks had returned to their natal streams to spawn. In total, 5.9% of the seine catch was marked. The proportion of marked fish increased over time from 5.0% in the first period to 13.2% in period 4 (Table 1). In all four periods, a higher percentage of females was marked. Sixty-six had been adipose clipped and 45 of those fish contained CWTs. Thirty-two of the tags were from Puget Sound sites, nine were from Fraser River sites, and four were from Strait of Georgia sites. We assumed that the adipose-clipped fish without tags were hatchery fish. The remaining marked fish had been finclipped (left or right pelvic) at several Canadian production facilities on the Fraser River and the Strait of Georgia. All marked fish that could be aged were of freshwater age 1. (1983 brood year and released in 1985). The freshwater age of nearly all of the unmarked juvenile coho was 1., but this proportion declined over time (Table 1). Two fish were aged 0., indicating that they had not spent a winter in freshwater. Forty-one fish had a freshwater age of 2.

The Pütter growth equation fit the size trajectories of most definable groups of coho (Table 2; Fig. 2). Maturing male coho were exceptional, since their growth appears to have accelerated over the summer (Fig. 2B) and the size trajectory was better fit by the exponential model. Male coho (excluding jacks) had significantly faster maximum growth rates than female coho salmon, but initiated growth later and, consequently, achieved a smaller asymptotic size than did females (Fig. 2A; Table 2). Combining the sexes and excluding jacks, marked coho grew significantly faster than unmarked coho but appear to have begun their growth trajectory at a smaller size and at a later

TABLE 2. Estimates of the two parameters of the linearized exponential growth equation (eq. 1) for jack coho and the three parameters of the Pütter growth equation (eq. 2) for other coho groups. Jacks were excluded from the latter groups. Numbers in parentheses are 95% confidence intervals. The jacks include fish from period 1 that were originally recorded as nonmaturing males but were subsequently reclassified (see text).

Sex	Group	n	a	K	r^2_{adj}
Male	Jacks	86	4.780 (4.614–4.946)	0.00377 (0.00305–0.00449)	0.556
			L_∞(mm)	K	t_0(doy)[a]
Male	Overall	1458	305.1 (304–306)	0.01164 (0.0115–0.0118)	106.4 (106–107)
	Unmarked	1379	306.6 (305–308)	0.01134 (0.0112–0.0115)	104.8 (104–106)
	Marked	79	286.7 (279–294)	0.01725 (0.0149–0.020)	130.0 (124–136)
Female	Overall	1573	337.5 (336–339)	0.00771 (0.0076–0.0078)	83.6 (82.7–84.5)
	Unmarked	1473	335.6 (334–337)	0.00786 (0.0079–0.0079)	84.6 (83.7–85.5)
	Marked	100	372.7 (362–383)	0.00579 (0.0055–0.0060)	69.4 (62.7–76.0)
Both	Overall	3031	319.4 (318–320)	0.00947 (0.0094–0.0096)	94.7 (94.5–95.8)
	Unmarked	2852	319.7 (318–321)	0.00942 (0.0093–0.0095)	94.7 (94.0–95.3)
	Marked	179	314.4 (308–321)	0.01034 (0.00973–0.0110)	103.4 (99.1–108)

[a] Day of year.

date (Fig. 2C; Table 2). Within the sexes, the differences in the growth trajectories of marked and unmarked fish are more pronounced. For males, marked fish grew considerably faster than unmarked fish but started growth considerably later and had a significantly smaller asymptotic size (Table 2). For females the opposite was true, with marked fish growing more slowly but having a greater asymptotic size and earlier start date (Table 2). Although the differences in parameter values are significant, the differences in the growth trajectories appear small (Fig. 2).

We caught a total of 1199 juvenile chinook salmon, mostly in the second and third sampling periods. A significant ($P < 0.05$) excess of males was caught in the first period (Table 3), but during the remaining periods the sex ratio was not distinguishable from 1:1. Chinook juveniles were harder to sex than coho, especially when small. We suspect that errors in sexing were frequent in period 1 and that most errors would have been the misclassification of females as males. Except in the first period, nearly all of the fish had a freshwater age of 0. The numbers of 1-yr-old fish changed little over the four periods. Consequently, the change in freshwater age composition between the first and second periods was probably due to the continuous arrival during July of freshwater age 0. fish that had left their natal streams approximately 90 d after emergence in February through April. A few maturing males were seen in periods 2 and 3 (Simpson and Kadowaki 1992). Unlike maturing coho juveniles, chinook jacks would not have spawned until the fall of the next year (i.e. at ocean age .1). Twenty-seven chinook (2.3% of the total seine catch) were adipose clipped and of these, 21, all aged 0.0, contained CWTs. Nineteen of the tags were from the 1985 release of 1984 brood year fish from the nearby Chemainus River, one was from the Cowichan River, and one was from the Chilliwack River. We assumed that all marked fish originated from hatcheries.

The size trajectories of all groups of chinook were best described by the exponential model (eq. 1). Because sizes of all groups declined in period 4 (Fig. 3) due to what we suspect was either the movement of larger juveniles out of Saanich Inlet in late September and October or the descent of larger individuals to greater depths, we calculated size trajectories over the first three periods only. There were no significant differences between male (excluding maturing fish) and female chinook (Table 4; Fig. 3A). There were insufficient data to calculate size trajectories of maturing chinook. The freshwater age 1. fish were significantly larger than age 0. fish throughout most of the summer (Fig. 3B), but their growth rates were statistically indistinguishable from the age 0. juveniles. Marked chinook juveniles were significantly larger than unmarked fish, but growth rates of the two groups did not differ significantly (Table 4; Fig. 3C). Since most of the marked fish originated in the Chemainus River hatchery, size and growth differences between marked and unmarked fish were possibly stock effects, rather than general hatchery effects.

Factors Affecting Vulnerability to Sport Gear

We approached 1278 fishing parties at the Tsartlip boat ramp, and 1180 (92.3%) agreed to participate in our study. We approached almost all of the parties launching at the ramp. Of the 331 juvenile coho and 133 juvenile chinook sampled at the Tsartlip ramp, we have complete fork length, sex, and age data for 283 coho and 120 chinook. Almost all of the incomplete records resulted from unreadable scales.

Depth and angling method

The estimated depth at which a fish was caught by sport gear and the method used were strongly related. Downriggers generally caught fish, especially older individuals, at depths greater then 30 m (Table 5). Fish caught by casting were generally at depths of less than 10 m (Table 5). Fish caught by simple trolling, jigging, or mooching tended to be at depths of 10–30 m (Table 5). Significant numbers of fish of both species and all ages were reported caught with simple troll gear and planers at depths greater than 30 m. For the reasons outlined above, we think it probable that fishermen overestimated their fishing depths with these two gear types and that most of the fish were caught at depths less than 30 m. Coho salmon, regardless of age, were caught at shallower depths than chinook salmon and for both species, fish that had been in the ocean for at least 1 yr were caught at greater depths than ocean age 0. fish (Table 5).

We did not question fishermen about the methods they might have used that were unsuccessful, and we did not question them about what their target species was. Consequently we cannot know with certainty whether the vulnerability of juvenile fish

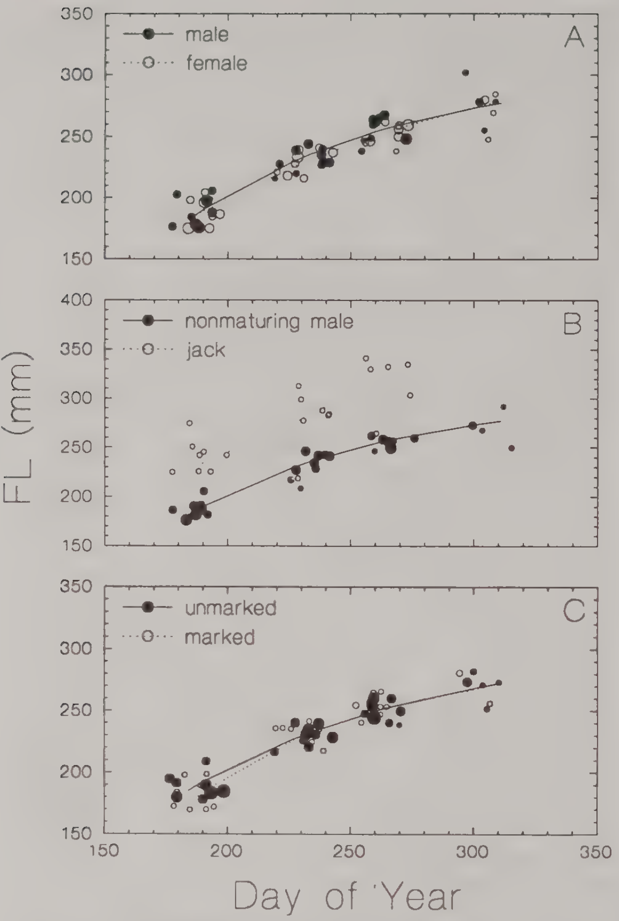

FIG. 2. Size trajectories for coho salmon grouped by (A) sex, (B) maturation, and (C) marking. Fitted lines are from Table 2. Each point is a daily mean, while the areas of the points are relative indicators of the sample sizes. The positions of all points have been "jittered" (a small random *x* and *y* value added to each point; Wilkinson 1988) to spread overlapping points.

varied between methods. We did examine this problem indirectly. If the vulnerabilities of juvenile fish and older fish were constant within methods, then the proportional catch by method for fish of ocean age greater than 0 as the expected, we calculated χ^2 tests of independence. For both species, the distribution of the catch by method for juveniles was significantly different from the expected (Table 5). The contribution of each method to the total χ^2 indicates which differences between observed and expected catches of juveniles were most important. Juvenile fish were more vulnerable to methods that used light gear at shallow depths (Table 5). Both juvenile coho and chinook were more vulnerable to simple trolling than were older fish. Juvenile coho were less vulnerable to downriggers and were more vulnerable to casting, while juvenile chinook were less vulnerable to planers (Table 5).

Sport-caught fish were consistently larger than fish of the same species, sex, age, and maturation state that were caught by seining. The size bias varied between methods. In the following tables the differences shown are statistically significant ($P < 0.05$). The numbers in parentheses are the sample size and the average difference between the observed fork length in the sport catch and the predicted fork length in the inlet population. The relationships between the sport fishing method and the bias in fork length for coho were jigging (39, 2.3 mm) < simple troll (185, 10.7 mm) < [planer (26, 11.5 mm) = casting (15, 14.9 mm) = downrigger (34, 19.4 mm) = mooching (5, 31.7 mm)] and for chinook were jigging (16, 2.7 mm) < [simple troll (74, 34.7 mm) = downrigger (28, 47.3 mm) = casting (3, 63.1 mm) = planer (4, 76.1 mm)].

Assumption of depth homogeneity of juvenile populations

Significant numbers of juvenile coho and chinook were reported caught in the sport fishery at depths greater than 30 m (Table 5), at least 6 m greater than the maximum fishing depths of our purse seines. By using all of the sport data in comparisons of the sport and seine catch, we have assumed that the characteristics of the juvenile coho and chinook populations were homogeneous over depth. We examined this assumption by comparing the characteristics of sport-caught juveniles caught at less than 30 m with the characteristics of those caught deeper. In more stringent tests of homogeneity, we looked for significant differences in characteristics in the three recorded depth strata.

Fork lengths within species and period were compared between the depth strata by one-way ANOVA. In 14 of 16 comparisons, no significant differences were found. Statistically significant variation of fork length with depth was present for coho salmon in period 2, with larger fish caught at greater depths. We examined the size distributions of sport-caught fish in the three depth strata and compared them with the distribution of fish caught in the seine samples from period 2 (Fig. 4). The average size of the sport-caught fish was larger than the average size of fish in the seine samples, regardless of depth, and size increased with depth in the sport-caught fish. However, the size range in the seine catch encompassed the sport-caught fish at all depths. For that reason, we think that the

TABLE 3. Numbers of juvenile chinook sampled and proportions of male (p_{males}), freshwater age 1. (p_1), and marked (p_{marked}) juvenile chinook in the seine and sport catches by period. $^*P < 0.05$, $^{**}P < 0.005$ H_0: proportions in seine and sport catches are equal (*G*-test).

Sampling period	n_{seine}	n_{sport}	p_{males} Seine	p_{males} Sport	p_1 Seine	p_1 Sport	p^{a}_{marked} Seine	p^{a}_{marked} Sport
1	61	2	0.754	—[b]	0.125	—[b]	0.098	0.0
2	643	17	0.533	0.647	0.016	0.667**	0.017	0.600**
3	357	99	0.504	0.566	0.045	0.704**	0.025	0.192**
4	138	15	0.500	0.600	0.058	0.600**	0.007	0.0
Overall	1199	133	0.532	0.579	0.034	0.692**	0.023	0.216**

[a] Proportion of freshwater age 0. fish only.
[b] Insufficient data.

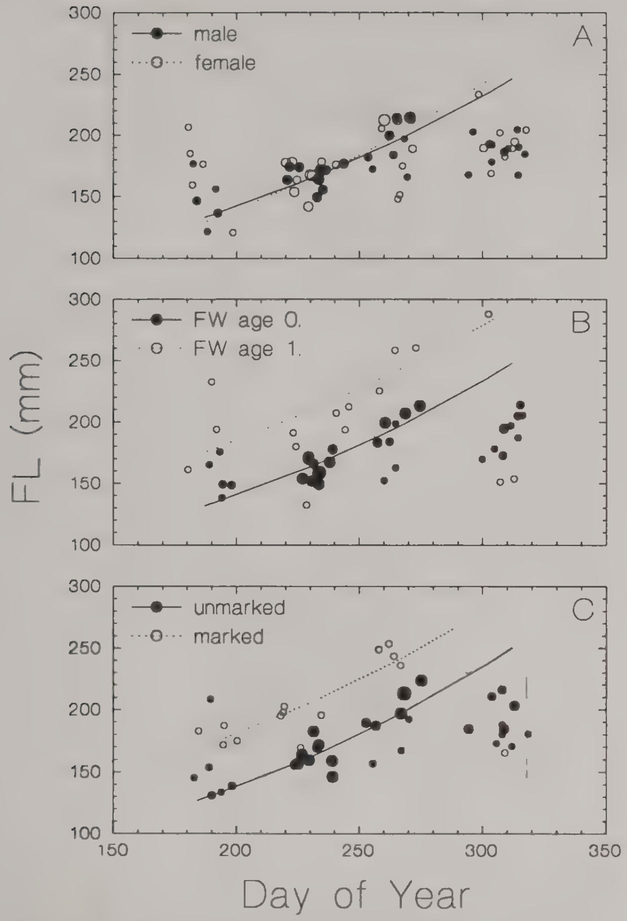

FIG. 3. Size trajectories for chinook salmon grouped by (A) sex, (B) freshwater age, and (C) marking. Fitted lines are from Table 4. Each point is a daily mean, while the areas of the points are relative indicators of the sample sizes. All points have been "jittered." Data for period 4 (days 287–320) were not fitted.

significant variation in size with reported depth of capture reflects an interaction of the size selectivity of fishing methods and the depths at which those methods are used, rather than real variation of size with depth.

Sex ratios, proportion marked, and freshwater age (chinook only) were compared within species both within periods and over all periods with *G*-tests. No significant differences were found for any of the comparisons. We conclude that the characteristics of the juvenile fish did not vary with depth and that the seine samples were representative of the populations sampled by the sport fishermen.

Size

Vulnerability to sport gear increased with size for the juveniles of both species. Sport-caught juvenile coho were larger than seine-caught coho of the same age in all time periods (Table 6). The difference in size between sport- and seine-caught fish declined over the study and was statistically significant ($P < 0.05$) only in the first three time periods. Sport-caught males were significantly larger ($P < 0.01$) than seine-caught males during the first two time periods, while females were significantly larger ($P < 0.05$) in sport catches during periods 2 and 3. A size-selectivity curve for sport-caught coho indicates strong selection for larger fish in periods 1–3 but no selection in period 4 (Fig. 5). The size selection threshold (the size at which vulnerability increased rapidly) increased from approximately 220 mm in period 1 to 250 mm by period 2 and 280 mm in period 3.

An increase in the size threshold could have resulted if a rapidly growing segment of the population was more vulnerable to sport gear, while the lack of size selectivity in period 4 might indicate the disappearance, from the inlet population, of that vulnerable population component. By period 4, coho jacks had disappeared from the seine catch, presumably having returned to their natal streams to spawn. Coho jacks were the largest fish in the seine-caught samples and were growing significantly faster than the other coho (Fig. 2). To test if the increase in the size threshold was due to the higher vulnerability of jacks, we compared the proportion of jacks in the seine catch and sport catch (Table 1), with the expectation of a higher proportion of jacks in the sport catch. We found that the proportion of maturing males in the sport catch was significantly higher than in the seine catch in period 2 but not in period 3 (Table 1). Recalculation of the selectivity curves excluding jacks partially removed the apparent size selectivity as indicated by the flattening of the size-selectivity curve over sizes from 180 to 270 mm (Fig. 5E compared with Fig. 5F). Thus, the size selectivity of the sport fishery for coho is partially explained by the higher vulnerability of the larger and faster growing jacks.

Large size significantly increased the vulnerability of juvenile chinook salmon to sport gear, since sport-caught chinook were significantly larger than seine-caught chinook in the last three time periods (Table 6). In part, the size differences resulted from the disproportionate catch of larger age 1.0 fish in the sport fishery (p_1, Table 3). Size-selectivity curves for sport-caught chinook (Fig. 6) indicate strong selection of fish greater than 200–250 mm. There is a weak indication that the threshold increased over time but the sample sizes in the sport catches of periods 1 and 4 were small.

TABLE 4. Estimates of the two parameters for the linearized exponential growth equation (eq. 1) for chinook salmon. Numbers in parentheses are 95% confidence intervals. $r^2_{\text{adj.}}$ has been adjusted for the degrees of freedom.

Group	*n*	*a*	*K*	r^2_{adj}
Overall	1061	3.909 (3.78–4.03)	0.00520 (0.0047–0.0057)	0.290
Male	563	3.907 (3.81–4.13)	0.00493 (0.0043–0.0056)	0.279
Female	492	3.828 (3.65–4.01)	0.00554 (0.0048–0.0063)	0.306
Freshwater age = 0	967	3.932 (3.81–4.05)	0.00507 (0.0046–0.0056)	0.283
Freshwater age = 1	31	4.399 (3.89–4.90)	0.00410 (0.0020–0.0062)	0.338
Unmarked	1029	3.869 (3.75–3.99)	0.00533 (0.0048–0.0058)	0.306
Marked	26	4.331 (3.96–4.70)	0.00433 (0.0028–0.0059)	0.557

TABLE 5. Depth distributions of sport-caught fish by fishing method, grouped by species and ocean age. For juvenile fish, expected totals were calculated from the catch, by method, for ocean age > .0 fish. The χ^2 values shown are given by (observed catch by method − expected)^2 / expected. *$P < 0.001$.

Depth range (m)	Fishing method						
	Trolling (powered boat)			Static			
	Simple	Planer	Downrigger	Mooching	Jigging	Casting	Total
Coho ocean age 0							
< 10	54	1	6	9	5	18	93
10–30	95	8	13	5	0	21	142
> 30	25	16	14	0	0	0	55
Total	174	25	33	14	5	39	290
Expected	140.2	43.6	77.9	—	—	9.3	
χ^2	8.2	7.7	25.9	—	—	94.1	136.1*
Coho ocean age > 0							
< 10	12	0	0	0	0	1	13
10–30	17	2	10	0	0	2	31
> 30	16	12	15	0	0	0	43
Total	45	14	25	0	0	3	87
Chinook ocean age 0							
< 10	15	0	2	2	0	1	20
10–30	39	0	17	1	0	15	72
> 30	18	4	9	0	0	0	31
Total	72	4	28	3	0	16	123
Expected	38.1	15.2	41.5	1.6	5.8	20.8	
χ^2	30.1	8.3	4.4	1.3	5.8	1.1	51.0*
Chinook ocean age > 0							
< 10	9	1	1	5	1	6	23
10–30	61	9	39	0	13	56	178
> 30	75	48	118	1	8	17	267
Total	145	58	158	6	22	79	468

Sex

The proportion of juvenile male coho salmon in the sport catch (all periods combined) was significantly greater ($G = 9.2$, $P < 0.01$) than the proportion observed in the seine catch (Table 1). Males were more abundant than females in the sport catch in all four periods and were significantly more abundant in the first two periods (Table 1). There were no apparent trends over the summer in the sex ratio in the sport catch.

The proportion of juvenile male chinook in the sport catch was consistently greater than the proportion in the seine catch, but never significantly so (Table 3). The powers of the tests were low, however, due to the small sample sizes.

Freshwater age

At least 60% of the juvenile chinook salmon caught in the sport fishery had a freshwater age of 1, although fish of that age comprised only 1.6–5.8% of the seine catch during the same periods (Table 3). The preponderance of older fish in the sport catch was probably due to their larger mean size (Fig. 3B) and the size selectivity of the sport fishery (Fig. 6). There were insufficient data for coho salmon to examine the effects of freshwater age.

Origin

Whether a fish was of wild or hatchery origin was a significant determinant of vulnerability in both species. For coho, the average proportion of marked fish in the sport catch was 0.109, nearly twice the proportion of marked fish in the seine catch (Table 1). The proportions of marked fish in the sport catch were significantly greater than in the seine catch in periods 2 and 3 and in the overall comparison (G = 6.47, 3.91, and 11.49, respectively, all $P < 0.05$). On average, the sport fishery removed marked fish from the population 1.99 times faster than unmarked fish. The proportion of marked fish in the sport catch did not vary much between periods. The proportion of marked fish in the seine catch was consistent for the first three time periods but doubled in the small sample from period 4 (Table 1).

Only a small part of the excess of marked coho in the sport catch was due to the higher vulnerability of jacks. If jacks are excluded, the proportion of marked fish in the sport catch (0.102, all periods) remains significantly ($G = 8.14$, $P < 0.01$) greater than the proportion in the seine catch (0.059). With jacks excluded, the sport fishery removed marked fish from the population 1.81 times faster than unmarked fish.

The proportion of marked juvenile chinook in the sport catch (0.068) was three times that found in the seine catch (0.023; $G = 6.96$, $P < 0.01$). In terms of relative exploitation rates, the sport fishery removed marked chinook three times faster than unmarked fish. Hatcheries release only fish of freshwater age 0, and in that age group, the proportion of hatchery fish in the sport catch was nine times higher than in the seine catch (Table 3). In terms of relative exploitation rates, the sport fishery removed marked juvenile age 0. chinook 11.8 times faster than unmarked chinook. Because only a small percentage of hatchery fish was tagged, it is likely that the sport catch of age 0.0 juvenile fish was predominantly of hatchery origin.

Marked chinook were larger than unmarked chinook in all periods (Fig. 3) and the sport fishery was strongly size selective (Fig. 6). Consequently, the higher proportion of marked chinook in the sport catch might have resulted from size selectivity

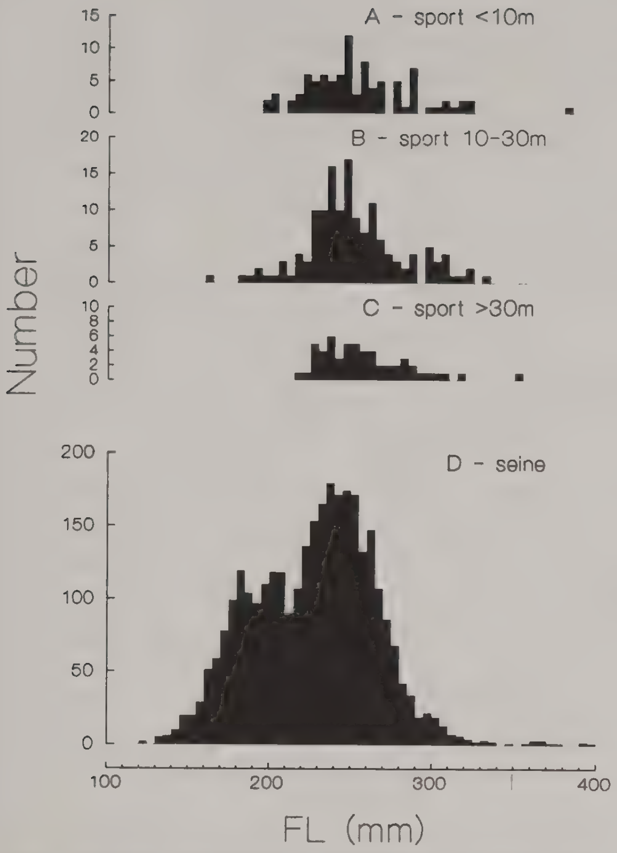

FIG. 4. Frequency distributions of fork lengths for juvenile coho in the three depth strata reported (A–C) in the sport catch and (D) in the seine catch during period 2.

alone. To examine this, we restricted the samples within each sampling period to fish at least as large as the smallest marked fish observed in the sport catch and repeated the comparisons. Because of the small sample sizes, only the overall comparisons were made. The proportion of marked fish in the seine catch increased to 0.036 (of $n = 446$) but remained significantly lower than the proportion in the sport catch (0.095 of $n = 95$; $G = 5.64$, $P < 0.05$). For chinook aged 0., the mark rate in the sport catch (0.62 of $n = 13$) remained significantly higher ($G = 32.3$, $P < 0.05$) than the mark rate in the seine catch (0.037 of $n = 408$). With the size restriction, the sport fishery removed marked fish at 2.8 times the rate of unmarked fish and removed marked age 0. juveniles 42 times faster than unmarked age 0. fish. Because of the small sample size in the sport catch, these results must be treated with caution, but it does appear that juvenile hatchery chinook were more vulnerable to the sport fishery regardless of size selectivity. There were no differences in the size of marked and unmarked coho, exclusive of jacks, so the size selectivity of the fishery did not affect interpretation of the results for that species.

Discussion

Most sport fishermen in Saanich Inlet seek large chinook salmon and use the heavy, deep fishing gear best suited for that species. The Inlet is not generally recognized as a major sport fishing area for coho salmon. It does appear, however, that it is a major rearing area, at least during the first summer and fall of ocean life. Godfrey (1968) noted in analyzing his seine catch data that there appeared to be a movement of juvenile coho and chinook from Cowichan Bay through Satellite Channel and into Saanich Inlet in June. Healey (1978) found that the highest concentration of juvenile coho in late summer was along the Vancouver Island shore in the Gulf Islands area. Saanich Inlet was one of two areas he highlighted as ''consistently good nursery areas.'' In our study, based on the CWTs recovered in both the sport and seine catches, it appears that lower Fraser River and Puget Sound coho migrate into Saanich Inlet by July and August to rear there until at least the fall. As a sheltered area close to a major urban center (Victoria), Saanich Inlet probably supports an ocean sport fishery typical of those in the lower Strait of Georgia and Puget Sound. However, there are other areas around the Strait of Georgia where coho salmon are the target species and where catches of juveniles are considerably higher (Shardlow and Collicutt 1989a, 1989b).

Juvenile salmonids use the upper water column throughout their first summer in the ocean (Pearcy and Fisher 1988; Shenker 1988; Brodeur 1989). Coho salmon in particular feed heavily on neustonic organisms, which are available only at depths of less than 5 m (Brodeur 1989). Nevertheless, a large proportion of the sport catch was reported caught at depths greater than 30 m. We have shown that there were no significant differences in size, sex, origin, or freshwater age with depth in the sport catch. Furthermore, difficulties in accurately estimating fishing depths while trolling with lead sinkers or planers, and difficulties determining when a juvenile had been caught with downriggers, probably led fishermen to overestimate the numbers of juvenile fish they had caught below 30 m. Fishermen did not report catching any juvenile fish while using any of the three methods where small fish can either be readily sensed on the line or where depths can be accurately estimated (Table 5). We conclude that our seine nets, which had maximum fishing depths of 20–24 m, were unbiased samples of the inlet populations of juvenile salmonids.

Argue et al. (1983) described a simulation model developed to aid the management of sport and commercial fisheries for chinook and coho salmon in the Strait of Georgia. The modelers acknowledged that their assumptions that all stocks were equally vulnerable to all segments of the fishery and that sport fisheries were neither size nor sex selective were arbitrary. Our results provide a basis for modifying those assumptions.

Juvenile fish appeared to be more vulnerable to simple troll gear and to casting and less vulnerable to downriggers or planers when compared with older fish. These differences in vulnerability were probably due to age-related changes in depth distributions. However, numerous older coho and chinook salmon were caught at depths less than 30 m (Table 5), indicating that older fish were present at shallow depths. This observation suggests that as they age, coho and chinook exploit deeper waters by expanding the depth range they use rather than by shifting to greater depths.

The vulnerability of juvenile coho and chinook salmon to sport fishing gear was highly size dependent. Initially only the largest individuals were vulnerable, and as the summer progressed, an increasing proportion of the resident fish recruited to the fishery and apparent selectivity decreased. The selectivity of sportfishing gear for juvenile coho was a linear function of fork length when jacks were included but was an exponential function of fork length when jacks were excluded. The size-selectivity curve was approximately exponential for chinook salmon. Although small juvenile chinook (<20–25 cm) were

TABLE 6. Results of approximate *t*-test to determine if the mean fork length (mm) of sport- and seine-caught juvenile coho and chinook, stratified by sex and time period, differed. There were insufficient data for chinook in period 1 for comparisons. $*P < 0.05$; $**P < 0.01$.

		Sport			Seine			
Sex	Period	*n*	Mean	SE	*n*	Mean	SE	*t*
Coho								
Male	1	18	243.1	29.5	569	190.3	23.2	7.5**
	2	82	250.5	29.2	449	238.5	22.6	3.6**
	3	77	264.7	30.8	469	259.8	29.4	1.3
	4	14	268.7	24.1	57	277.1	21.9	1.2
Female	1	7	207.4	27.2	525	187.1	21.0	2.0
	2	62	237.3	18.1	491	230.2	19.4	2.9**
	3	60	260.7	21.4	499	254.1	19.8	2.3*
	4	7	287.3	20.6	56	273.7	17.2	1.7
Both	1	25	233.1	32.7	1094	188.8	22.2	6.8**
	2	144	244.8	25.8	940	234.2	21.4	4.7**
	3	137	262.9	27.1	968	256.9	25.1	2.5*
	4	21	274.9	24.2	113	275.4	19.7	0.1
Chinook								
Male	2	11	228.7	15.9	343	165.0	26.8	12.7**
	3	56	250.9	34.9	180	203.7	38.1	8.6**
	4	9	247.0	43.5	69	194.4	31.6	3.5**
Female	2	6	214.0	37.4	300	163.1	22.6	3.3*
	3	43	252.1	37.3	177	207.5	34.6	7.1**
	4	6	274.2	23.4	70	195.2	32.2	7.7**
Both	2	17	223.5	25.4	643	164.1	24.9	9.5**
	3	99	251.4	35.8	357	205.6	36.4	11.2**
	4	15	257.9	38.3	139	194.8	31.8	6.1**

less vulnerable to sport gear than coho of the same size, the vulnerability of chinook juveniles increased at a faster rate than coho as the fish became larger. The exponential rise of vulnerability with size for chinook salmon resulted in a disproportionate number of the larger, age 1.0 chinook being caught in the sport fishery. Since age 1.0 chinook were predominantly of wild origin, the negative effects of the sport fishery on wild production may be greater than total catch rates indicate. Because age 1.0 chinook originate from northern and interior stocks rather than coastal stocks, the impact of the sport fishery is heavier on what are potentially the least productive wild stocks. Furthermore, differential effects on one freshwater age class of a novel and significant mortality source might be modifying, to the detriment of long-term productivity, the selective environment within which the complex mix of chinook life history strategies (Healey 1983, 1986a) evolved.

Sexual maturation state may also have affected vulnerability. Male juvenile coho were proportionally more abundant in the sport catch than in the seine catch and were generally larger than females. The overrepresentation of males was partly due to the presence of jacks in the sport catch, and part of the bias in sex composition was probably due to size selectivity. However, jacks were clearly growing faster and along a different size trajectory than were nonmaturing males and females. We speculate that their faster growth was associated with more voracious feeding. Differences in the vulnerabilities of maturing and nonmaturing fish to a hook and line fishery may reflect different foraging strategies. Healey (1986b) has observed that the commercial troll fishery for coho salmon off the west coast of Vancouver Island catches an excess of female salmon. Holtby and Healey (1990) speculated that such sex-specific mortalities in coho were a consequence of differing feeding rates and consequent levels of risk-taking adopted by the sexes. A similar explanation may underlie the apparent difference in the behavior of maturing and nonmaturing male coho, adding further complexity to the within- and between-population differences in sex-specific growth rates, and presumed foraging behaviors, described by Holtby and Healey (1990).

The proportion of hatchery-marked fish in the sport catch was significantly higher than in the seine catch for both coho and chinook salmon. The proportion of marked coho in the sport catch was twice that in the seine catch, while the proportion of marked age 0.0 juvenile chinook salmon in the sport catch was nine times greater than in the seine catch. Expressed in terms of relative exploitation rates, the sport fishery was removing marked juvenile coho 1.99 times faster than unmarked fish and removing marked juvenile chinook about three times faster than unmarked fish. If the effects of freshwater age and size selectivity on the vulnerability of chinook are considered, then the sport fishery may have been removing marked age 0. chinook 42 times faster than unmarked fish. We conclude that during their first summer in the ocean, hatchery fish of both species are more vulnerable to the sport fishery than are wild fish.

For coho salmon, the size selectivity of the sport fishery and the consequent overrepresentation of jacks in the sport catch explained only a small part of the higher vulnerability of hatchery fish in the sport fishery. Thus, the faster growth of coho salmon in hatcheries compared with the wild, and the resulting increase in the proportion of male coho that become jacks (Bilton et al. 1982), does not significantly affect the relative vulnerabilities of hatchery and wild fish to angling. In chinook salmon, the larger and more vulnerable juvenile fish were aged 1.0, and were almost entirely of wild origin. Consequently, the

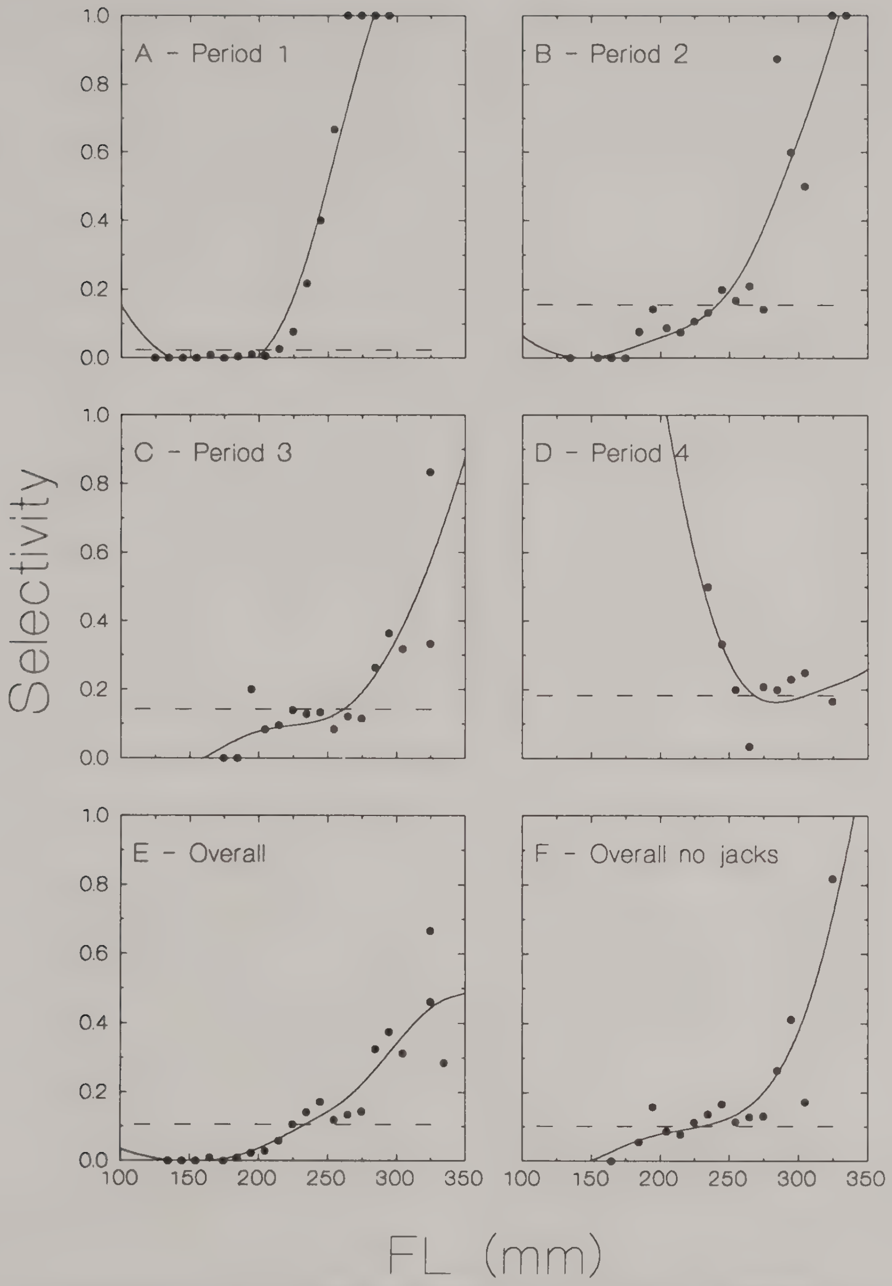

FIG. 5. Size-selectivity curves for juvenile coho salmon (ocean age 0) caught by sportfishing gear in Saanich Inlet for (A–D) sampling periods 1–4 in 1985, (E) over all periods, and (F) over all periods excluding jacks. The lines are DWLS smoothing functions. The ratio between the total sport catch and the total seine catch for the appropriate group and period is indicated by the horizontal broken line in each panel and indicates an absence of size selectivity.

size selectivity of the sport fishery may have reduced the apparent difference between the vulnerability of hatchery and wild chinook in the sport fishery.

We do not know why juvenile hatchery fish, and especially hatchery chinook, were more vulnerable than wild fish in the sport fishery. Hatchery fish may be voracious but inexperienced and incautious feeders, accustomed to life in the risk-free and food-rich environment of a hatchery. As juveniles, hatchery fish may be more aggressive than wild fish (Swain and Riddell 1990), and consequently may be more voracious. Voracity coupled with inexperience may have heightened vulnerability to a hook and line fishery, where the fish must pursue a lure.

An inverse relationship between potential growth rate and vulnerability to hook and line fisheries may be a general phenomenon in fishes. Raat (1985) observed that fast-growing common carp (*Cyprinus carpio*) were more likely to be hooked than were slow-growing individuals. Kleinsasser et al. (1990)

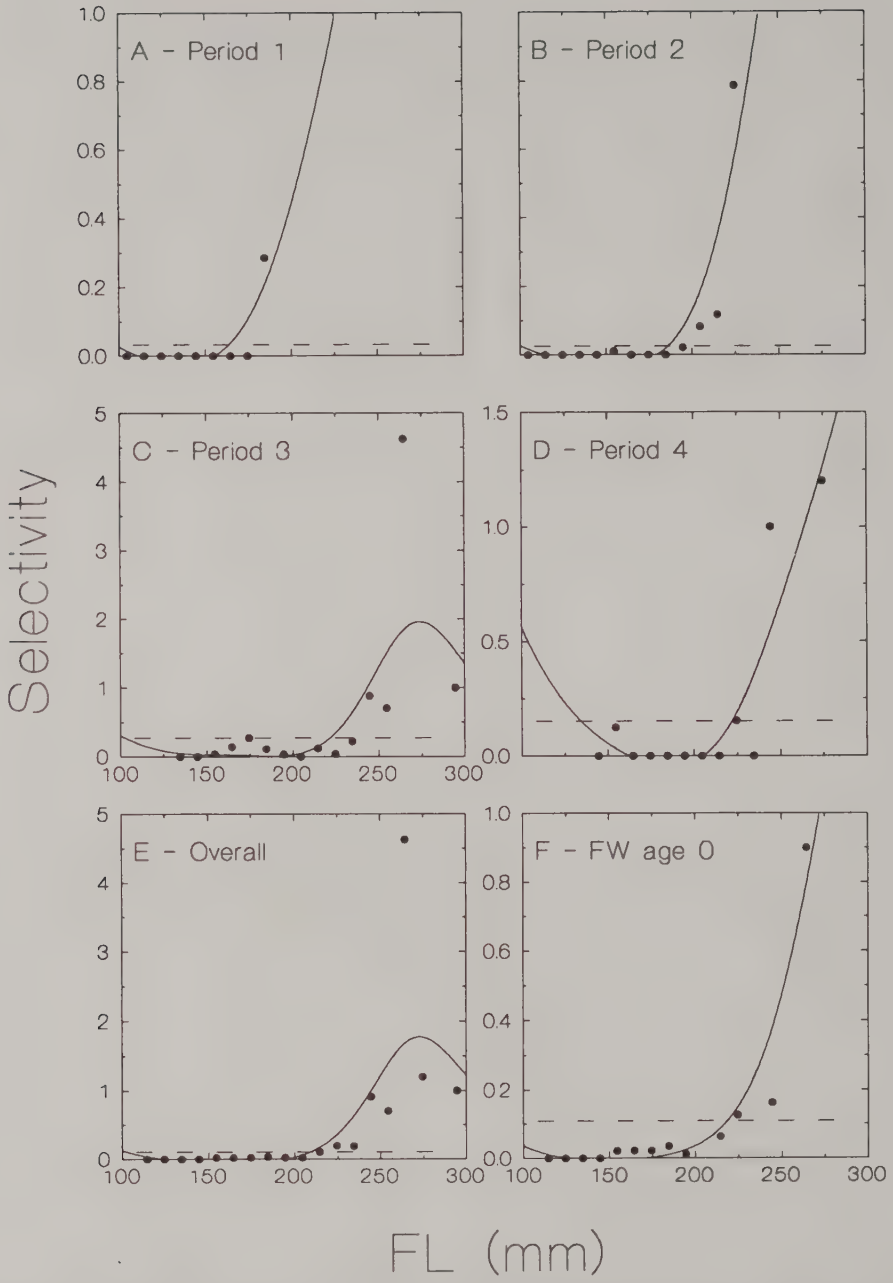

FIG. 6. Size-selectivity curves for juvenile chinook salmon (ocean age 0) caught by sportfishing gear in Saanich Inlet for (A–D) sampling periods 1–4, (E) over all periods,and (F) for freshwater age 0. fish only. The lines are DWLS smoothing functions. The ratio between the total sport catch and the total seine catch for the appropriate group and period is indicated by the horizontal broken line in each panel and indicates an absence of size selectivity.

found that fast-growing strains of largemouth bass (*Micropterus salmoides*) were more vulnerable to angling than slow-growing strains. In two comparative studies of several strains of rainbow trout (*O. mykiss*) the faster growing strains, which were also the domesticated strains, were more vulnerable to angling and had lower survival rates exclusive of the fishery (Brauhn and Kincaid 1982; Dwyer and Piper 1984). Potential rather than realized growth rates appear to be more important in affecting vulnerability, since in some studies, domesticated strains, which grow faster than wild strains under hatchery conditions but not in the wild, are more susceptible to angling (Pawson and Purdom 1987; Dwyer 1990). Differences in the vulnerabilities of domestic and wild strains are probably genetic and not the result of growth histories (Pawson and Purdom 1991). Thus, the positive relationships between growth rate, domestication, and vulnerability to angling may underlie our observations if one of the consequences of intensive hatchery culture of Pacific salmon has been the selection of fast-growing strains.

Because we were not sampling closed populations and there were likely size-dependent fish movements, we think it unlikely that our size–time trajectories estimate individual growth in either species. Nevertheless, there is some evidence suggesting that hatchery coho smolts did not grow as well as wild smolts during their first 2 mo in the ocean. Wild coho smolts entering the ocean from the east coast of Vancouver Island in the vicinity of Saanich Inlet do so in mid- to late May at an average weight of 8–15 g (L. B. Holtby, unpubl. data). Hatchery smolts are released in early to mid-May at average weights of ≈25 g. Thus, wild fish enter the ocean later, and at a smaller size, than hatchery fish. To account for the observed sizes of juvenile coho in Saanich Inlet in July, it is necessary to assume that hatchery fish grew slowly for some period of time after ocean entry and during that time, wild smolts overtook them in size. Presumably, as they gained experience in the wild, hatchery fish began to feed more efficiently and their growth accelerated so that by midsummer (our second sampling period), marked fish were the same size as unmarked fish and were growing significantly faster. Differences in the growth constant in marked and unmarked juvenile chinook were not significant. However, comparisons between wild and hatchery chinook were compromised by the low marking rates for chinook, the small sample size in the sport fishery, and the possibility that differences were due to a stock effect rather than a general effect of hatchery culture.

An important consequence of the higher vulnerability of hatchery salmon to angling may be that marine survivals in hatchery populations are lower than those in wild populations. However, the evidence for lower marine survivals in hatchery populations is ambivalent. In this study, the proportion of marked chinook in the inlet population did decrease over the summer (Table 3). Declining abundance of juvenile hatchery chinook relative to wild chinook may have been caused by greater vulnerability in the sport fishery and, consequently, higher mortality. However, the proportion of marked coho increased over the summer (Table 1). Sport fishermen were seeking adult chinook in Saanich Inlet which we think resulted in catches of juveniles that were small compared with the observed population sizes.

In situations where wild fish and hatchery fish derived from the same population smolt from the same river, hatchery populations do appear to have lower marine survivals. In their study of an enhanced coho stock (incubation and rearing in a hatchery but released from a natural spawning area), Schubert and Lister (1986) observed a higher total exploitation rate for the enhanced coho than for naturally produced coho (81.5 versus 72.6%) and a lower overall smolt to adult survival rate (12.4 versus 16.3%). They attributed a part of the difference in exploitation rate to biases in the escapement estimates attributable to higher straying rates of the cultured fish, but speculated that the earlier maturation and run timing of the naturally produced fish might have led to their lower availability to ocean fisheries. Such differences in exploitation rate would also result if the differences in vulnerability that we demonstrate for juvenile fish persisted to the adult stage. The cultured fish may also have been more vulnerable to sport fisheries during their first 6 mo at sea. The large numbers of juvenile salmon that are caught and released in the Strait of Georgia (English et al. 1986; Farlinger et al. 1990) and significant mortality rates for hooked and released juvenile fish suggest that differential vulnerability to sport fisheries might, at least partially, account for lower survivals of hatchery fish. In a comparison of a wild and hatchery population on the Chehalis River, WA, marine survivals for the wild population were generally higher than those for the hatchery population (Seiler 1989). However, in studies where marine survivals are compared over larger geographic areas, there are no consistent differences between wild and hatchery populations (LaBelle 1990; Cross et al. 1991).

The apparent difference in the vulnerability of wild and hatchery coho and chinook salmon in a sport fishery has important implications. Many management models include estimates of shaker mortality (e.g. Argue et al. 1983). We have shown that coho and chinook salmon reared in hatcheries are more vulnerable to sport fisheries during their first summer in the ocean. If, as we suspect, hatchery fish behave differently from wild fish during their first few months of ocean life, then the use of hatchery fish as models for wild fish in terms of ocean survival or ecology is questionable. Studies of early ocean ecology in areas where significant proportions of the smolts are from hatcheries (e.g. Fisher and Pearcy 1988; Pearcy and Fisher 1988, 1990; Brodeur and Pearcy 1990) may not be applicable to wild fish. Furthermore, much of what we think we know about the distribution of wild salmon in the ocean and the rates at which they are exploited by fisheries has been derived from CWT programs at hatcheries. If the differences in vulnerability persist in older fish, stock and fishery assessments that rely exclusively on hatchery CWT data would consistently overestimate the effects of the fishery on wild stocks. Investigations into the ecological significance and the spatial and temporal stability of our results would be natural extensions to this study.

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Bias in Hydroacoustic Estimates of Fish Abundance due to Acoustic Shadowing: Evidence from Day–Night Surveys of Vertically Migrating Fish

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Appenzeller, A. R., and W. C. Leggett. 1992. Bias in hydroacoustic estimates of fish abundance due to acoustic shadowing: evidence from day–night surveys of vertically migrating fish. Can. J. Fish. Aquat. Sci. 49: 2179–2189.

We investigated the hypothesis that fish schooling behavior leads to underestimation of fish abundance when assessed by acoustic methods. Current methods for acoustic quantification of fish abundance rely on the assumption that fish biomass and numerical fish abundance are linearly related to acoustic scattering under all natural fish densities. However, cage experiments as well as field observations have indicated that acoustic shadowing effects occur at very dense and large aggregations of fish. Acoustic surveys of the pelagic fish community of Lake Memphremagog, Quebec, were conducted when fish were aggregated and dispersed. These differences in aggregation were related to diel responses to light levels. We found that estimates of fish abundance, as measured by echo integration, were consistently and significantly lower when fish were aggregated in dense schools. This bias was not due to diel changes in average echo level per fish, which exhibited no relationship to diel changes in vertical and hortizontal distributions. We conclude that the reduced abundance estimates obtained when fish were aggregated resulted from acoustic shadowing. Our data suggest that this bias may be as large as 50%.

Nous avons examiné l'hypothèse selon laquelle le comportement en bancs du poisson conduit à une sous-estimation de l'abondance par les méthodes acoustiques. Les méthodes courantes de mesure acoustique de l'abondance du poisson sont fondées sur l'hypothèse selon laquelle la biomasse et le nombre de poissons sont en relation directe avec la diffusion acoustique, peu importe la densité naturelle du poisson. Toutefois, les expériences faites en enclos, ainsi que les observations sur le terrain, ont indiqué que des effets d'ombre acoustique apparaissent lorsque les poissons sont réunis en grand nombre et en forte densité. Les relevés acoustiques de la communauté nectonique en milieu pélagique du lac Memphrémagog, Québec, ont été faits lorsque le poisson était réuni en bancs et lorsqu'il était dispersé. Ces variations dans le degré de regroupement ont été mises en rapport avec les réponses nychtémérales à l'intensité de l'éclairement. Nous avons constaté que les estimations de l'abondance du poisson, telles qu'obtenues par échointégration, étaient constamment et significativement inférieures lorsque le poisson était réuni en bancs denses. Cette erreur systématique n'était pas attribuable à des changements nychtéméraux de l'intensité moyenne de l'écho par poisson, qui ne semblaient pas être en rapport avec les variations nychtémérales de la distribution horizontale et verticale des populations. Nous sommes parvenus à la conclusion que les estimations moindres de l'abondance, obtenues lorsque le poisson était réuni en bancs, résultaient de l'ombre acoustique. Les résultats de nos travaux indiquent que cette erreur systématique pourrait atteindre 50 %.

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Hydroacoustic methods are being used increasingly in freshwater and marine systems to quantify fish abundance and biomass. The accuracy of acoustically derived abundance data depends largely on established empirical relationships between echo strength and units of fish size or fish biomass (Love 1971, 1977; Foote 1987). The echo integration approach to abundance assessment has been proposed as the standard method (Johannesson and Mitson 1983; MacLennan 1990) because it can be applied in situations where echos from single fish, or from aggregations, are measured. An important unresolved question, however, is whether the relationship between fish abundance and echo signal, quantified as integrated echo values, is independent of the nature and intensity of fish aggregation in typical field survey situations or whether echo measurements must be adjusted for bias related to fish aggregation (Foote 1983; Toresen 1991). Current calibration methods assume that fish aggregation has no influence on the integrated echo (Johannesson and Losse 1977; Foote 1983; Bayona 1984).

In an attempt to answer this question, Roettingen (1976) and Foote (1983) conducted experimental studies on caged fish. Their investigations led to conflicting conclusions. Foote (1983) reported a linear relationship between echo intensity and fish biomass under all fish densities measured. In contrast, Roettingen (1976) found echo intensity to be linearly related to fish abundance only at lower fish densities. At high fish densities, a "shadowing effect" was observed, which resulted in underestimation of fish biomass (Fig. 1). Field investigations into the nature of this relationship have also produced conflicting results. Aglen (1983) reported that fish biomass estimates were generally lower when fish were dispersed during nighttime surveys. He concluded that these differences were related to the different echo thresholds he applied. However, Bazigos (1975), Gerlotto (1989), and Soria and Freon (1991) have all reported

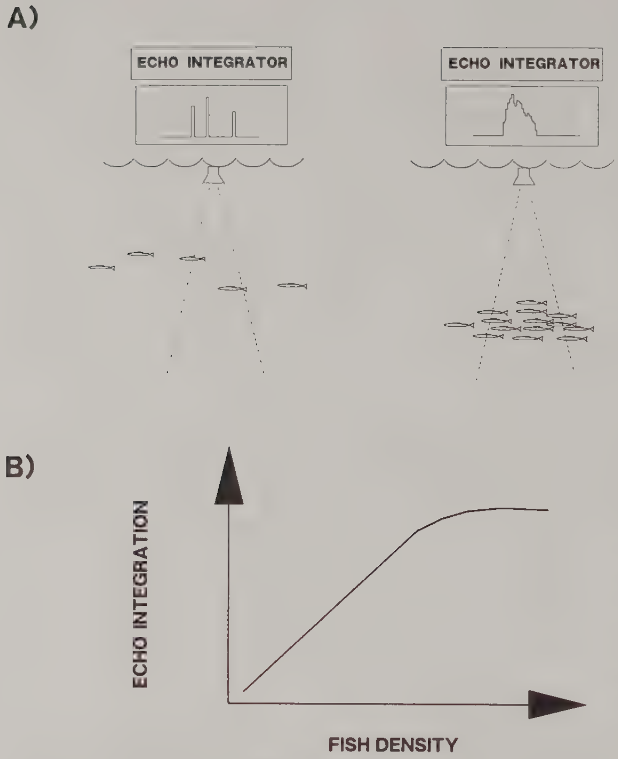

FIG. 1. (A) Ensonification of fish that are dispersed (left) and schooled (right) and resulting echo signals. When fish are dispersed, echo signals are separated and appear as single spikes (one for every fish). When fish are schooling, a multiple echo is received (from many fish ensonified together). (B) Generalization of Roettingen's (1976) study that suggested a linear relationship between true fish density (number of fish in the experimental cage) and echo integrated estimates of density made at low fish densities. At high fish densities the echo integrated values reached a plateau.

that acoustic estimates of biomass were more frequently higher when fish were dispersed at night, relative to when they were aggregated during the day. Bazigos (1975) and Soria and Freon (1991) hypothesized that vessel avoidance by schooling fish during daylight hours (as observed by Olsen et al. 1983a), combined with acoustic shadowing effects (Gerlotto 1989), may have produced these results. Toresen (1991) quantified the absorption of acoustic energy in relation to fish density in herring schools and observed that increasing fish density was associated with a loss in bottom signal intensity, thereby providing direct evidence of shadowing at high fish densities. The resolution of these conflicting results lies in acoustic surveys where the effects of fish avoidance and the effects of acoustic shadowing can be separated.

In addition to possible problems associated with shadowing in dense schools, the question arises whether the average target strength (TS) of fish remains constant when fish change their depth during diel vertical movements, a behavior commonly associated with changes in aggregation (Dembinski 1971; Blaxter 1975; Woodhead 1966). Such depth-related effects, together with changes in the tilt angles of fishes at day and night (Buerkle 1983), could explain the observed variability in day–night acoustic estimates of fish numerical abundance and biomass (Foote 1983).

Major uncertainties regarding the accuracy of acoustic estimates of fish numbers and biomass may also occur if the vertical distribution of fishes and the diel changes in their distribution are not known prior to sampling (Shotton and Bazigos 1984). This occurs because some fish in the targeted population could be inaccessible to the acoustic beam either by being at the surface (Thorne 1977) or near the bottom (Burczynski et al. 1987) where acoustic signals are unreliable.

TABLE 1. Comparison of experimental and model fish densities using Pitcher and Partridge's (1979) fish school model.

	Roettingen (1976)		Foote (1983): herring
	Sprat	Saithe	
Observed mean fish length (cm)	12.1	35.1	27.1
Observed range of fish densities (fish/m^3)	100–3500	10–350	14–57
Observed acoustic shadowing effects (fish/m^3)	1800–2600	100–130	None
Predicted range (model) of fish densities (fish/m^3)	560–880	23–36	50–80

In the in situ study reported here, we sought to evaluate the direction and magnitude of biases in hydroacoustic estimates of fish numerical abundance and biomass resulting from changes in fish aggregation. Specifically, we sought to rigorously evaluate Roettingen's (1976) hypothesis that fish aggregation leads to underestimation of fish biomass when assessed by hydroacoustic methods.

Natural Fish Densities and Acoustic Shadowing Effects Reported in the Literature

We first addressed the question "Are natural densities of schooling fish within the range of fish densities in those experimental studies in which acoustic shadowing effects were observed?" Resolution of this question is important because shadowing effects have been observed only under very high fish densities, below which a linear relationship between echo scatter and fish abundance seems to occur (Roettingen 1976). Additionally, experimental comparisons of small (12 cm) and large (35 cm) fish have revealed that shadowing effects occur at the much higher densities characteristic of smaller fishes (Roettingen 1976).

To assess this question, we used Pitcher and Partridge's (1979) empirical model, which relates schooling fish densities to fish body size. This model is based on comparisons of observed nearest neighbor distances between schooling fishes and the corresponding volume inhabited by a single fish within the school. We calculated the water volumes occupied by individual fish within a school by applying two factors, one for dense schools (factor 0.6) and one for looser aggregations (factor 1) (see Pitcher and Partridge 1979) (Fig. 2). Using this approach, we compared the fish sizes and densities used by Roettingen (1976) and Foote (1983) in their experimental studies with the fish densities predicted for equivalent sizes using the Pitcher and Partridge (1979) model (Table 1; Fig. 2).

This comparison indicates that Roettingen's (1976) experiments were conducted at fish densities that included the range of densities predicted by the Pitcher and Partridge (1979) model. However, his maximum densities where shadowing effects occurred greatly exceeded the maximum predicted by the model using a factor of 0.6. Foote's (1983) experiments, in contrast, were clearly conducted at fish densities that matched only the

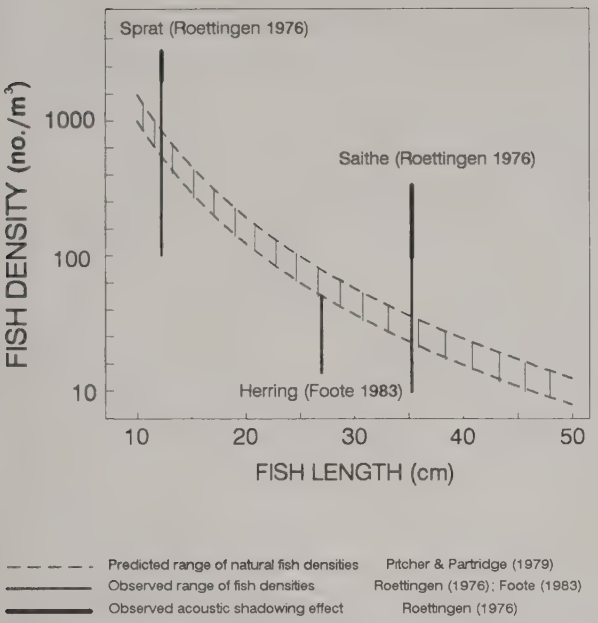

FIG. 2. Graphic representation of Pitcher and Partridge's (1979) model relating fish size (length) to fish density (logarithmic scale). The model densities are indicated by broken lines, the lower line indicating low levels of fish aggregation (factor 0.6) and the upper line indicating high density polarized schools (factor 1). Superimposed are experimental ranges of caged fish densities used by Roettingen (1976) and Foote (1983) to assess whether changes in fish densities result in deviations from a linear relationship between echo density and integration estimates of density (medium-sized line). The heavy line depicts the range of fish densities at which Roettingen (1976) observed shadowing effects.

lower limits of the natural fish densities predicted from the model. This suggests that Foote's (1983) conclusion that echo scatter is a strictly linear function of the in situ fish biomass may have resulted from his failure to investigate a sufficiently wide range of fish densities.

Toresen's (1991) study, however, supports the conclusion that acoustic shadowing effects may exist in situations where aggregations are very large. His data show that bottom echo strength was a negative function of the vertical extention of the fish layer above. This finding strongly supports Roettingen's (1976) conclusion that acoustic shadowing is related not only to density effects, but also to the total number of fish within the acoustic beam. Given that natural schools may occupy volumes many metres to perhaps hundreds of metres in vertical and horizontal extent, a large number of fish can be ensonified simultaneously by a single echo wave (Toresen 1991). The echo return from such a wave might be considerably altered in strength and time delay, as a consequence of the development of variable acoustic wave paths within the fish school due to multiple reflectance of the sound energy.

In situ Studies

Study Area

We selected the Central Basin of Lake Memphremagog, Quebec–Vermont, as our study site for the in situ trials. Lake Memphremagog has a total surface area of 83 km^2, is long (40 km in the south–north direction) and narrow (average width 2.4 km), and contains three distinct basins that differ in mean depth (South Basin 6.9 m, Central Basin 50.9 m, and North Basin 13.5 m) (Fig. 3). The Central Basin is the deepest part of the lake and approximates 110 m. This basin has a surface area of 20.5 km^2 and accounts for almost two thirds of the total lake volume. The basin is an elongated (15 × 2 km), deep trench with very steep shorelines. Waters of depths <30 m represent less than 10% of the total basin surface area (Fig. 4). The depth and the shoreline steepness of this basin provided almost unlimited acoustic access to its pelagic fish population, which is dominated by rainbow smelt (*Osmerus mordax*), a species known to school by day and disperse at night (Dembinski 1971; Argyle 1982; Heist and Swenson 1983; Burczynski et al. 1987).

We used vertical net hauls operated from deep water to the surface (net opening area 9 m^2) to identify and to calibrate acoustic signals. This method worked well at night, but did not yield fish catches during the day when fish distribution were highly patchy (Fig. 5). Only rainbow smelt were caught. The dominant length class captured was 12 cm total length (TL) (SD 1.8). A smaller but less abundant size class averaging 5 cm TL also occurred in our catches. During early summer, larval and young-of-the-year juvenile smelt (average length 2–3 cm) were observed and caught in the upper water layers (maximum 10 m depth). Young-of-the-year smelt were captured with a 1-m^2 net with 2-mm mesh size. In these trials, we used only vertical hauls made during darkness. Echosounder records showed that these young-of-the-year smelt did not perform diel vertical migrations. Rather, they remained in the epilimnion during both day and night. They were therefore separated vertically from the larger fish. The abundance and dominant size categories of smelt captured in our nets were consistent with size and abundance estimates obtained acoustically immediately prior to net sampling.

In addition to these catch-based identifications, we were also able to visually identify adult smelt that were attracted to the surface in large numbers by strong flashlights shone at the water surface at night during spring.

The transparency of the water in the study area was measured by Secchi disk and an underwater light meter. Over the course of the investigation (July–September of 1988 and 1990), Secchi depths were 4–8 m. Direct measurements of light levels (microwatts per square centimetre) to depths of 30 m indicated that the depth at which 1% of the underwater surface light remained (lower limit of the phototrophic zone) varied between 9 and 13 m over the course of this study. Light levels at other depths were calculated using water column extinction coefficients and surface light intensities.

Acoustic Techniques

We used a 120-kHz Biosonics model 105 dual-beam echosounder (beam width 11 and 25°) to quantify the numerical abundance and biomass of pelagic fishes. The system was mounted in a 18-ft outboard-powered boat. The transducer, which was mounted in a V-fin towing body, was suspended by bungy cords from a davit. This mounting effectively dampened wave-induced motion of the transducer, which was towed at a depth of 1 m. Power was supplied from a gasoline-powered electric generator. Boat speed during all surveys was maintained at 8.5 km/h. During night sampling, all lights were extinguished to avoid attraction or disturbance of the fish. We obtained an estimate of total fish biomass of the pelagic fish population through echo integration of 20 log *R* amplified sig-

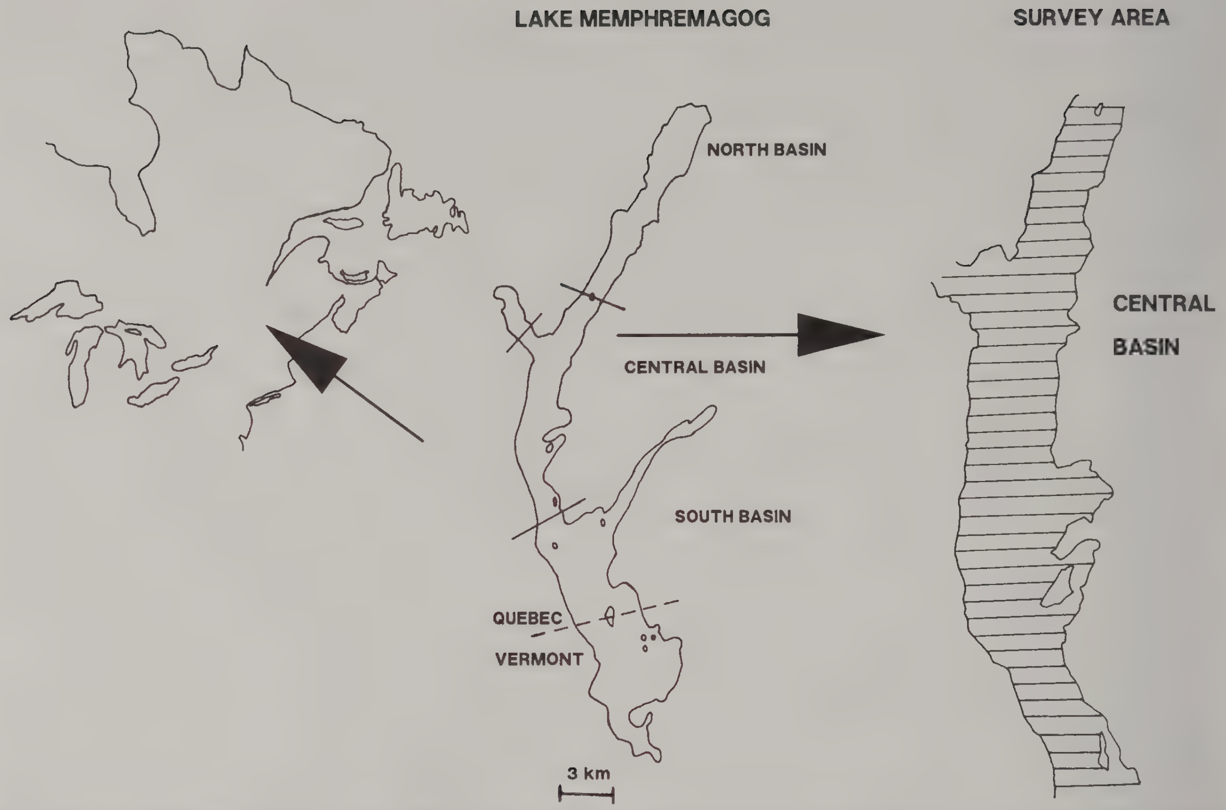

FIG. 3. Lake Memphremagog, Quebec–Vermont. The study area used to estimate acoustic fish abundance is shown on the right. This area was subdivided into 40 parallel transects from which 12 were selected at random for each complete survey (for a detailed description of the procedure, see the text: Survey Design).

nals. We also quantified the average size of the targets by analysis of 40 log R dual-beam signals. During all surveys, we used 20 log R and 40 log R amplifications on alternate pings. The ping rate was 5/s and the pulse length was 0.4 and 0.8 ms. All acoustic signals were recorded for subsequent analysis using a Biosonics recorder interface coupled to a VCR. All data analysis was performed on these recorded data. Depth-related noise peaks at 100 m depth were generally $<$50 mV at 20 log R amplification and ranged from 100 to 200 mV at 40 log R amplification. We used the same receiver gain factor at +6 dB for both day and night surveys. The maximum voltages recorded from dense schools were $<$8 V. Echo integrated data were processed at 50 pings per sample interval. This equates to a linear scale of 45–50 m. Relative fish densities were expressed as volts squared per square metre of lake surface area (Fig. 6A). Fish density figures presented in this paper are either averages obtained from spatial intervals of 50 m (Fig. 6A) or averages based on complete transects of length 1–2 km (Fig. 7). We excluded signals from the top 10 m from the analysis because we found these waters to be inhabited principally by smaller nonmigrating larval and juvenile fish. In order to quantify diel vertical distribution patterns of fish, the echo integration processor was subdivided into 1-m depth windows, and density values were averaged across a complete transect (Fig. 6B).

Survey Design

Continuous sampling of a single transect

We used two different survey designs. First, we adopted an approach in which a single transect was ensonified repeatedly over 12 or 24 h (Fig. 8). This provided continuous information on diel changes in fish distributions. It also yielded comparative estimates of fish abundance obtained at a single transect location when smelt were alternately aggregated and dispersed (day and night). The data used in these investigations were collected during July–September of 1988 and 1990. During these periods the surface waters of the lake exceeded 18°C and a strong thermocline was established at depths ranging from 5 (early July) to 15 m (mid-September). The thermocline blocked the vertically migrating smelt from entering the warm surface layer at night. In late summer with depths of the thermocline exceeding 10 m, it also prevented movement of smelt into the shallow South Basin of Lake Memphremagog (Fig. 4A). During the day, smelt schools were located in deeper water but remained well above the lake bottom (Fig. 5). They were, therefore, continuously accessible to the acoustic beam.

Whole-basin estimates

We next conducted surveys designed to yield estimates of the total number of pelagic fish in the Central Basin. These investigations were conducted from mid-July to early September of 1990. We conducted biweekly day and night surveys, in total, nine during the day and seven at night. A particular day survey was followed within 24 h by a night survey or vice versa (see Fig. 9 and 10: calendar day of surveys). To estimate the number of fish in the Central Basin, we selected 12 parallel, east–west transects at random from a total of 40 predetermined, equally spaced lake segments that covered the entire Central Basin (Fig. 3). We ensonified these 12 transects within an

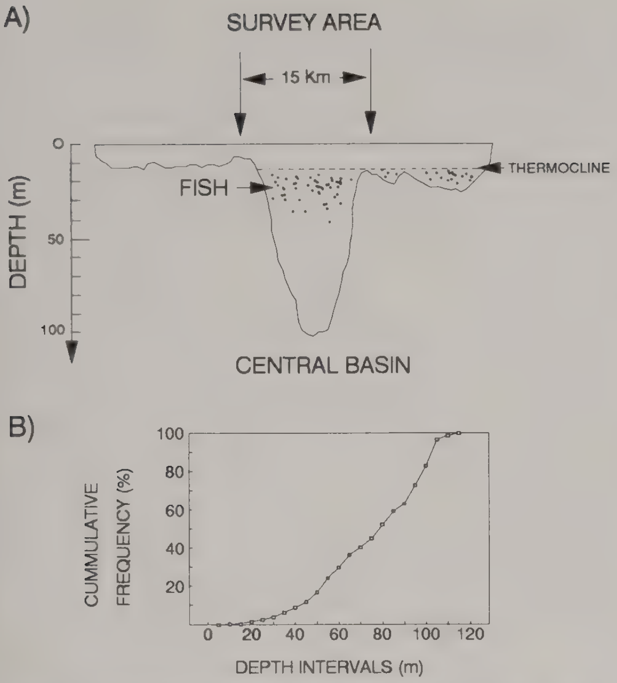

FIG. 4. (A) Morphology across Lake Memphremagog. A typical summer fish distribution (dots) below the thermocline (broken line). (B) Cumulative depth distribution in the Central Basin survey area as derived from acoustic depth records of 12 transects ($n = 4000$ soundings).

interval of 4–5 h. To avoid damage to the boat and the transducer, we avoided water depths <5 m near the shore. Generally, the 5-m depth contour was located within 20 m of the beach. Throughout our investigations the thermocline was located between 8 and 10 m depth. We estimated fish biomass by echo integration. These acoustic data were averaged over 50-m spatial intervals. The total survey consisted of 360 to 400, 50-m averages located along the 12 transects. The average transect length was 1400 m. Estimates of fish biomass were calculated using only full transect data ($n = 12$ per survey) and were computed from the average acoustic level per survey. For these analyses, we used 20 log R amplified echo signals, which were processed by a digital echo integrator. All individual transect means were weighted by the corresponding transect length because transects varied in length.

We calculated the average acoustic size of individual fish by processing 40 log R amplified echoes and computing the average TS for all fish ensonified on each survey using standard Biosonics processing. This method is based on echo signals obtained from two channels (dual-beam echosounding) using only targets selected as single fish echos. For additional information on this technique see Ehrenberg (1984) and Burczynski and Johnson (1986). To transform acoustic sizes (TS) into units of fish length, we used the general relationship for TS and fish length established by Love (1977):

$$\mathrm{TS} = 18.4 \log (l) - 1.6 \log (f) - 61.6$$

where TS = target strength in decibels, l = length of fish in centimetres, and f = frequency in kilohertz.

We used this equation, despite the evidence (Rose and Leggett 1988) that the relationship for TS and fish length can be highly variable among species because, in our study, the exact relationship for smelt was not known. This possible inaccuracy, however, does not influence our results, which are entirely based on relative changes in acoustic fish sizes during day and night.

To convert echo integration estimates into estimates of fish biomass, we derived scaling factors based on the average TS of the fish surveyed. This approach is described in detail in Burczynski and Johnson (1986). We determined mean TS for each survey. The average calibration factor (16 surveys) to convert the integrated echo data from units of volts squared per square metre to fish per square metre was 0.6.

Results

Diel Patterns of Spatial Distribution

Repeated continuous acoustic sampling along a 2-km transect provided information on diel changes in fish distribution and acoustic estimates of fish abundance. As previously noted, the pelagic fish population of Lake Memphremagog's Central Basin is dominated by rainbow smelt. Consistent with earlier observations (Dembinski 1971; Argyle 1982; Heist and Swenson 1983; Burczynski et al. 1987) these smelt exhibited distinct diel patterns of schooling and vertical displacement that are most likely related to the light levels and the thermal structure of the water column (Evans and Loftus 1987). The first component of this diel pattern, vertical displacement of the fish, resulted in the following day–night patterns: fish were located in midwater (30–50 m) during the day, well off the bottom, and moved up to depths adjacent to the thermocline (10–20 m) at night. The second component of the day–night pattern consisted of a change in aggregative behavior: during daylight hours, smelt aggregated in dense schools. During the night, smelt were more dispersed into regular scattering layers (Fig. 5 and 6). The transition between these distinct day and night patterns occurred at twilight.

Measurements of surface ambient light energy during daytime, together with measurements of light absorption in the water column as a function of depth, were used to calculate light levels at the depths where fish schools were located during acoustic surveying. We found that schooling smelt were usually found at depths with light levels $<0.01\ \mu\mathrm{W/cm}^2$ during day surveys. These values refer to the 50th percentile of the fish biomass distribution with depth and are calculated on the basis of complete transects.

Day–Night Replicates

Measurements of echo scatter (quantified by echo integration) yielded estimates of fish abundance that increased at sunset, peaked at night, decreased near sunrise, and were at their lowest during daylight hours (Fig. 8). To statistically evaluate these trends, we compared echo integration abundance estimates derived from replicated transects surveyed within a single 24-h period. Fourteen of 17 such day–night comparisons had higher echo scatter (higher estimated abundance) during the night (Table 2). The mean echo scatter and calculated fish density during night surveys was significantly greater than that of day surveys (paired t-test: $t = 2.89$; df = 16; $p = 0.011$). A regression model using estimates of fish density during daylight hours as the dependent variable and estimates of fish density during darkness as the independent variable revealed a significant ($p = 0.001$; $r^2 = 0.53$; $n = 17$) positive relationship (Table 3; Fig. 7). Although the intercept was not significantly different from zero, the slope of this regression (0.53) was significantly ($p < 0.01$) different from 1.

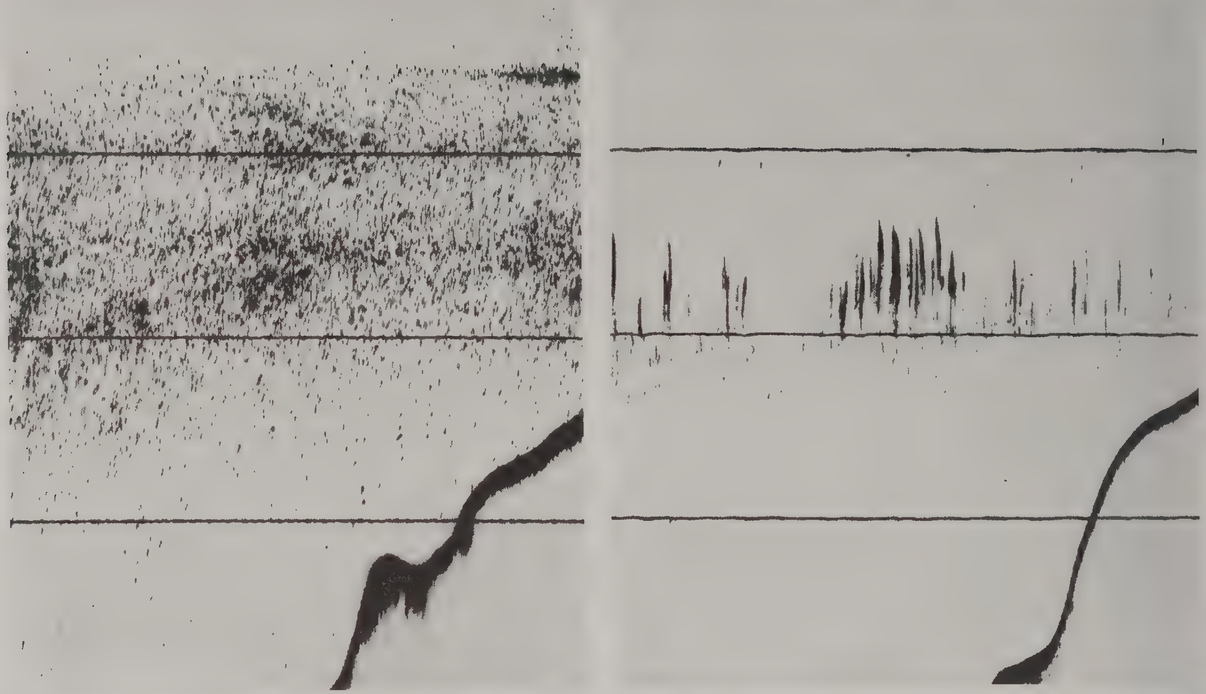

FIG. 5. Echo chart of an identical transect across Lake Memphremagog during the night (left) and during the day (right). Fish are dispersed in the water column at night (single signals) and are aggregated in schools during the day. The dark band on the right lower corner is the lake bottom signal. The vertical scale is indicated by 20-m depth lines. The horizontal scale is highly compressed with a total length of approximately 2 km.

Quantitative Surveys of Fish Abundance

Acoustic fish size measurements

During the summer of 1990, we conducted 16 quantitative acoustic surveys of the Central Basin. During each, we estimated average fish size and fish abundance acoustically in the basin during both day and night. The selection of single echos to determine fish size was performed using Biosonics echo shape criteria for single fish echos. Day surveys yielded fewer single fish echos than did night surveys because of the tendency for smelt to school during daylight. On average, we obtained 1111 (SD 1122) single echos per day survey and 2711 (SD 1327) single echos per night survey. Covariance analysis of the average strength of single echoes in relation to day, night, and season was conducted. We applied a multiple regression model to the acoustic data using fish size as the dependent variable and a day–night dummy variable (day = 0; night = 1) as the treatment effect. The covariate was season, expressed as calendar day. The interaction between treatment (day–night) and covariate (calendar day) was not significant ($p = 0.46$). The covariance analysis revealed (Table 4; Fig. 9) (1) no significant difference in average acoustic fish length between day and night ($p = 0.57$) and (2) no significant change in average acoustic fish length over time ($p = 0.38$).

Day–night whole-basin estimates of fish abundance

Our analysis of acoustic fish size led us to conclude that observed variations in average TS were not a product of day–night or seasonal influences. We therefore calibrated our acoustic fish abundance data (echointegrated values in volts squared per square metre) for each survey using the average scaling factor (0.6 fish/V^2) derived from all surveys ($n = 16$).

To assess the influence of day–night and seasonal changes in fish behavior and abundance on acoustic fish estimates, we conducted an analysis of covariance by applying a multiple regression model to our acoustic data. We used estimated fish abundance as the dependent variable and a day–night dummy variable (day = 0; night = 1) as the treatment effect. The goal of this analysis was to determine whether acoustic fish abundance changed significantly between day and night. We used calendar day as a covariate for fish abundance in order to determine seasonal changes in fish abundance. Before conducting the analysis of covariance, we tested for significant interactions between covariate and treatment by applying a multiple regression model with fish abundance as the dependent variable treatment effect (day–night) and covariate (calendar day) and interaction term (day–night variable × calendar day) as independent variables. We found that the interaction term was not significant ($p = 0.39$), so it was dropped from further analysis. The analysis of covariance with treatment variable (day = 0; night = 1) and covariate (calendar day) revealed that the treatment effect and covariate were highly significant ($p < 0.001$) with an overall r^2 value of 0.86. This analysis revealed (Table 5) that (1) fish abundance increased with time during the study ($p < 0.001$) and (2) estimates of numerical abundance were significantly ($p < 0.001$) lower during the day than during the night (Fig. 10).

Summary of Results

We observed that acoustically derived estimates of fish abundance were significantly lower during the day than at night (Tables 3 and 5). These differences were consistent in the results of our two different survey designs: (1) repeated acoustic sur-

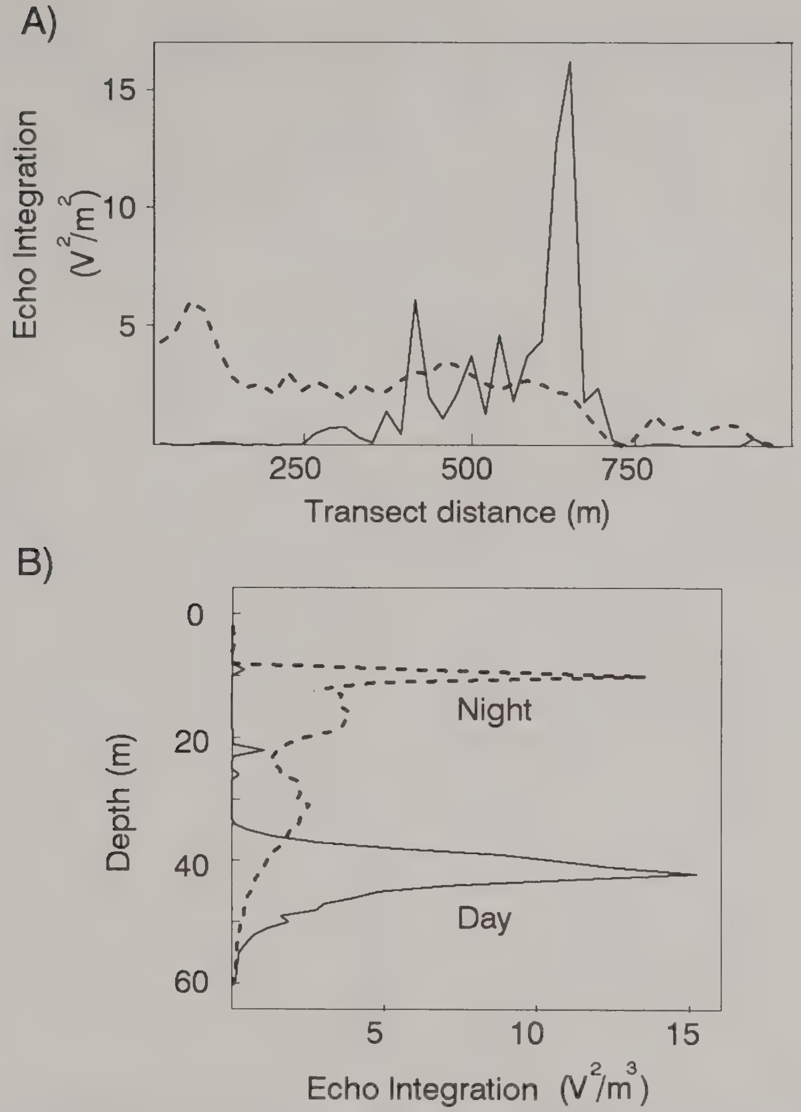

FIG. 6. (A) Typical day–night changes in the horizontal distribution of fish derived from the echo signal of a transect sequence (values averaged over 50 m and over all depths). During the day (continuous line), high variability of acoustic values derived from schools was prevalent. During the night (broken line), less variable data due to dispersion of fish were obtained. (B) Diel vertical distribution patterns of fish in Lake Memphremagog averaged across a transect (August 22, 1988). Echo integration values are separated into 1-m depth intervals (day = continuous line; night = broken line).

veying of a single transect during day and night (Fig. 7 and 8) and (2) acoustic estimates of fish abundance in the entire basin during day and night (Fig. 10).

Spatial patterns of fish differed between day and night (Fig. 5 and 6). Distributions were consistently highly aggregated and patchy during daylight hours and were highly dispersed at night. The measured acoustic differences were not due to day–night differences in the availability of fish to the beam because throughout the study the fish remained within a thermal refuge and could be targeted with our sampling gear with equal effectiveness during day and night. We also found that diel vertical displacement of the fish, which coincided with the diel change in patchiness, did not result in significant changes in the average TS for solitary fish (Table 4; Fig. 9). These data clearly indicate that the day–night differences in measured fish abundance cannot be explained by depth-related changes in behavior that result in changes in the average TS of fish.

The illumination levels at the depths occupied by fish during daylight hours were very low (<0.01 $\mu W/cm^2$; depth = 30–40 m). The observed differences in acoustic measurements were not, therefore, a consequence of diel differences in fish avoidance of the survey vessel.

We therefore conclude that the lower estimates of fish abundance consistently obtained when surveys were conducted during daylight were caused primarily by diel changes in fish aggregation and, in particular, the dense schooling of these fish during daylight hours. In two separate analyses (24-h surveys along single transects and day–night whole-lake surveys), our

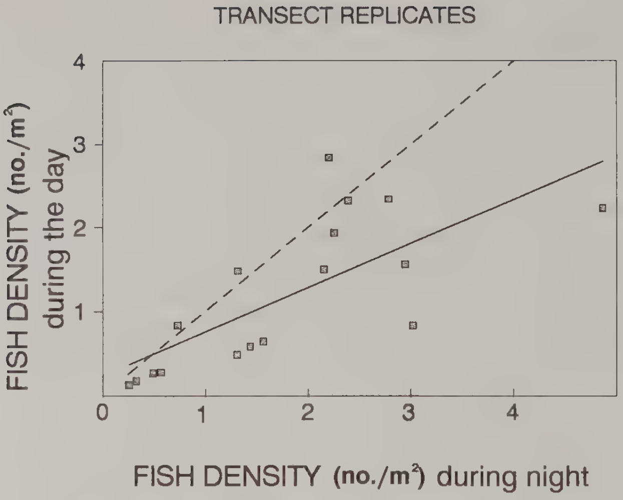

FIG. 7. Mean night and day hydroacoustic estimates of fish density, obtained during day–night surveys, conducted over 24 h on identical transects. Fish densities are averaged across the complete transect (continuous line = regression).

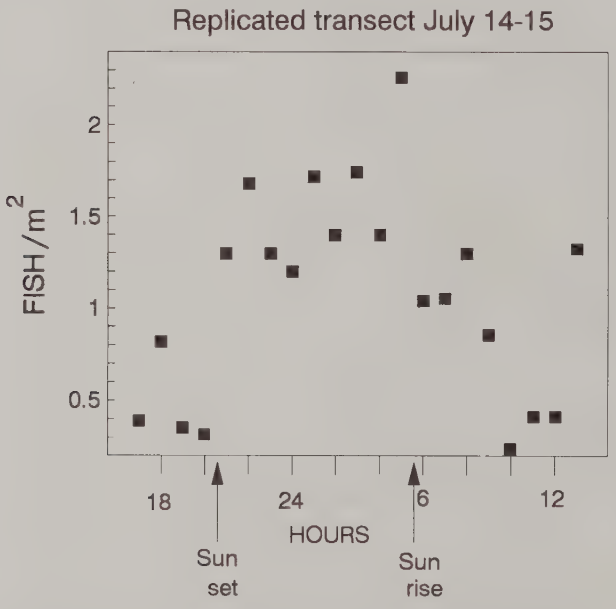

FIG. 8. Fish density as measured repeatedly along a single transect over 24 h on July 14–15, 1988. The day–night pattern is typical of that observed during 24-h studies conducted during June–September of 1988 and 1990.

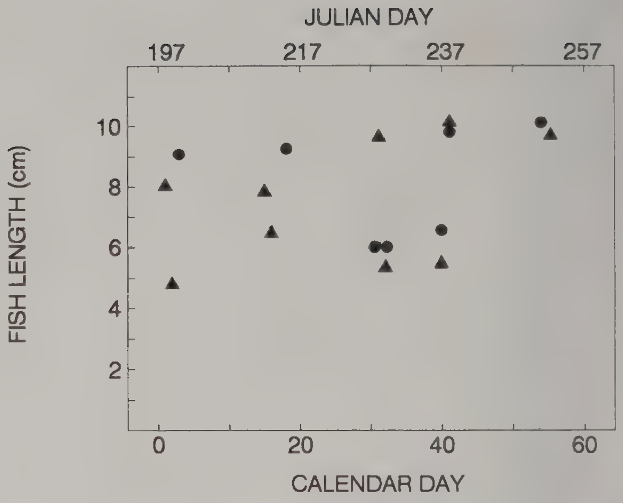

FIG. 9. Hydroacoustic estimates of mean fish length (TS) obtained from surveys of the Central Basin of Lake Memphremagog conducted throughout the summer of 1990 (circles = night surveys; triangles = day surveys).

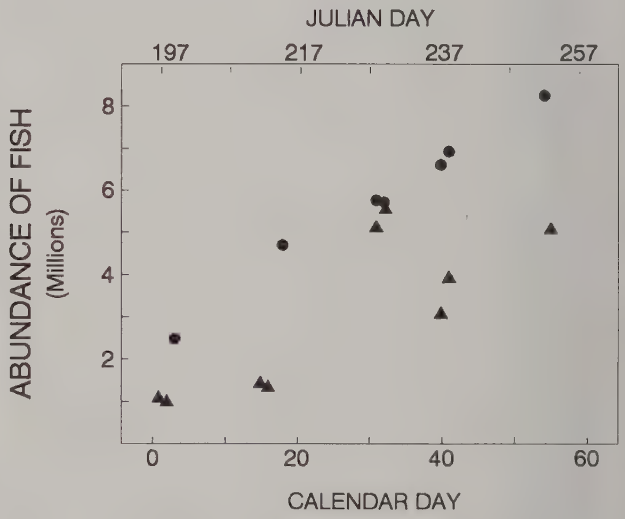

FIG. 10. Hydroacoustic estimates of the number of fish for the Central Basin of Lake Memphremagog obtained from acoustic surveys conducted during the summer of 1990 (circles = night surveys; triangles = day surveys).

data indicate that acoustic abundance estimates obtained by ensonifying fish during the day averaged approximately 50% (Fig. 7 and 10) lower than estimates obtained by ensonifying fish at night.

Discussion

Evidence for Acoustic Shadowing of Fish in Aggregations

These findings fully support Roettingen's (1976) hypothesis that acoustic shadowing can lead to a significant underestimation of fish abundance when the acoustic backscatter is generated by dense schools. The question arises as to whether day–night differences in acoustic scatter can be causally linked to this effect and whether it will be possible to generalize these findings. The answers to these questions are critical for any attempt to model and correct biases in fish abundance estimates resulting from acoustic shadowing. Bazigos (1975), Gerlotto (1989), and Soria and Freon (1991) have hypothesized that day–night differences observed in their acoustic studies were mainly the result of bias introduced by fish avoidance during the day. This hypothesis is supported by Olsen et al. (1983a, 1983b) who observed that schools of fish avoid survey vessels by swimming to greater depths. They further suggested that flight reactions of fish increase with their

TABLE 2. Fish densities (average fish/m^2). A comparison of day and night estimates for replicated transects within 24-h periods.

	Day	n	Night	n	Year
	0.50	3	1.31	2	1988
	1.50	4	1.32	3	
	0.60	2	1.44	5	
	0.66	5	1.57	5	
	0.85	3	3.03	1	
	2.25	1	4.87	1	
	1.58	3	2.95	2	
	1.52	2	2.16	4	
	2.86	9	2.21	2	
	1.95	2	2.26	2	
	2.34	6	2.40	2	
	2.36	4	2.79	5	
	0.85	5	0.73	5	1990
	0.14	3	0.26	4	
	0.28	6	0.49	5	
	0.29	4	0.57	4	
	0.19	3	0.33	3	
Mean	1.22	17	1.81	17	
SD	0.89		1.22		

TABLE 3. Day–night differences of replicate transects. Model: fish/m^2 during day = A (constant) + B (fish/m^2 during darkness).

Variable	Coefficient	SE	p
A	0.26	0.28	0.36
B	0.53	0.24	0.001
	$r^2 = 0.53$	$n = 17$	

ANOVA

Source	SS	df	MS	F-ratio	p
Regression	6.66	1	6.66	16.8	0.001
Residuals	5.94	15	0.40		

TABLE 4. Analysis of covariance: test for differences in day–night effects on acoustic fish size. Model: acoustic fish size = A (constant) + B (day = 0; night = 1) + C (calendar day).

Variable	Coefficient	SE	p
A	−48.667	1.102	0.000
B	0.633	1.095	0.57
C	0.030	0.032	0.38
	$r^2 = 0.10$	$n = 16$	

ANOVA

Source	SS	df	MS	F-ratio	p
Regression	6.33	2	3.17	0.69	0.52
Residuals	59.79	13	4.60		

proximity to the surface and are also stronger as survey vessel speed increases. However, Olsen et al. (1983a) also reported that "a comparison between day and night observations did not indicate any great difference in reaction patterns." It is questionable, therefore, whether observed day–night differences in acoustic estimates in general, and specifically those in our study, could be attributed to the flight reactions of fish.

In fact, contrary to expectations derived from the avoidance hypothesis, our abundance estimates were greatest during night when the fish were located near the surface (i.e. in closer proximity to the survey vessel). Flight reactions related to vessel avoidance, which typically consist of fish escaping to greater depths, should produce marked changes in average echo levels because the tilt angle of the fish in the acoustic beam will change (Olsen et al. 1983b). While such effects may also occur when fish are very close to the surface and the survey vessel, we observed no significant changes in average TS between day and night surveys during the more than 3-mo duration of our study in 1990. This may be because the fish studied were typically located at least 10 m below the surface at night and even deeper during the day (25–40 m) and were therefore not disturbed by the boat. In general, there are two ways in which fish can detect the presence of survey vessels: acoustic signals ("noise") and visual signals. We observed that during darkness, the fish we studied showed no obvious flight reactions to avoid boat noise (motors). This might be explained by the fact that most fish species are sensitive only to frequencies below 2000 Hz, the major exception being the cypriniform fishes (Myrberg 1978). Our survey vessel was small (18 ft), and both the boat and generator were powered by high-frequency motors, unlike vessels used in ocean surveying (Olsen et al. 1983b). Because the fish we surveyed were closer to the surface (approximately 10 m) during the nighttime surveys, and because these surveys yielded higher abundance estimates, it is unlikely that noise disturbance could be responsible for the day–night differences in the fish abundances we observed.

TABLE 5. Analysis of covariance: test for differences in day–night effects on numerical fish abundance. Model: numbers of fish = A (constant) + B (day = 0; night = 1) + C (calendar day).

Variable	Coefficient	SE	p
A	643 046	464 185	0.189
B	2 215 864	461 909	<0.001
C	93 642	13 629	<0.001
	$r^2 = 0.86$	$n = 16$	

ANOVA

Source	SS	df	MS	F-ratio	p
Regression	0.68×10^{14}	2	0.34×10^{14}	41.41	<0.001
Residuals	0.11×10^{14}	13	0.82×10^{12}		

Finally, it is very unlikely that the fish surveyed in our study were disturbed by visual signals because all light sources were extinguished during night surveys. We had, in fact, observed that smelt can be attracted by a strong flashlight or by illuminating the watercolumn for several minutes. It could, of course, be hypothesized that during the day, fish located at depths between 30 and 40 m could see the survey vessel and react. This hypothesis can also be rejected because light transparencies in the study area were insufficient to allow visual detection of the boat by fish. Secchi depth extinctions conducted during our investigation generally occurred at depths between 4 and 8 m, while the depth at which smelt schools occurred during daylight hours (30–40 m) typically had light levels <0.01 μW/cm^2. It is very unlikely that smelt could see a 5-m boat from a depth of 30 m at such low illumination. Woodhead (1966) noted that "even in oceanic waters maximum sighting ranges of fish would probably be little more than 35 m, and that for most fish they will be much less than 17 m even in good conditions." Blaxter (1980) has demonstrated that sighting distances of fish are reduced dramatically under the influence of both low illumination levels and high beam attenuation in the water column related to turbidity. His estimate of the sighting distance for fish under the light intensity and turbidity measured in Lake Memphremagog at depths where smelt occur is 2.3 m (beam attenuation coefficient 0.4; light intensity <0.01 μW/cm^2). We observed that smelt schools, when ensonified during daylight hours, exhibited flight reactions to a video camera lowered from the boat only when the camera was within approximately 5 m of the schools.

Physiological factors have also been hypothesized to influence day–night differences in acoustic abundance estimates. Foote (1983) hypothesized that the average TS may change during diel vertical migrations. Changes in swim bladder volumes with depth could, for example, produce lower average TS for fish in deeper waters. However, this would also lead to negative buoyancy with a corresponding requirement for swimming or changes in the tilt angle to compensate for sinking. It is not clear whether these effects occur and whether the combined reactions would result in lower average TS. Ona (1990) has shown that the average TS of fish may vary considerably for a species. He found that factors such as the degree of gut filling and body fat content can lead to natural variations in acoustic TS. While such sources of variance in acoustic TS may occur, our data, obtained over 3 mo of surveys, revealed no such day–night or seasonal variation.

We conclude, therefore, that the day–night differences in estimates of fish abundance we observed resulted from acoustic shadowing related to the aggregating behavior of the fishes we studied. Toresen (1991) also showed that acoustic shadowing occurs in natural aggregations of herring.

Consequences for Calibration of Acoustic Data

Our data strongly support the hypothesis that acoustic shadowing occurs when fish are densely aggregated (Fig. 1). This, in turn, implies that acoustic scattering is linearly related to fish abundance only when fish are not aggregated in dense schools. The assumption of a linear relationship between fish abundance and acoustic scattering is central to current hydroacoustic assessment methods. A reassessment of methods currently used for scaling echo integrated measurements is thus necessary. The currently used scaling methods are as follows.

(1) Single fish signals are counted from an acoustic monitor to establish a relationship between numbers of fish and echo integrated values measured coincidently (Midtun and Nakken 1977; Bayona 1984). These derived calibration factors, which relate echo levels and real fish units, are then applied to acoustic measurements without reference to the aggregation patterns of fish. Since single fish cannot normally be counted from the multiple fish echo typically derived from a school, this method lacks proof of validity. For example, Johannesson and Losse (1977) found a discrepancy between calibration factors derived by counting single fish and by direct calibration of acoustic measurements conducted on fish caged in nets with "more relevant fish densities." They wrote that "the net cage constant was about 30% higher than that obtained from the counting method." They concluded that "this discrepancy observed does not permit a conclusive explanation." Our findings strongly suggest that this phenomenon may have resulted from acoustic self-shadowing of fish when aggregated.

Haug and Nakken (1977), when relating trawl catches to echo integrated values, observed that results deviated with respect to fish density levels. They hypothesized that "large differences in relative units between fish catches and acoustic values are probably caused by a systematic underestimation of low fish densities when using trawls." Our findings suggest the alternative hypothesis that at high fish densities the echo integrated values could be too low, resulting in underestimation of fish abundance.

(2) The average TS is estimated by dual-beam or split-beam acoustic devices and is used to scale the integrated echo values (Bayona 1984; Burczynski and Johnson 1986). Here, too, the assumption is that the total echo signal strength measured from a school equals the sum of the signals from the individual fish being ensonified. Our results clearly indicate that this approach is invalid when fish occur at high densities. The calibration factors we derived from TS measurements failed to yield identical estimates of fish biomass and numerical abundance of fish in a day–night comparison. Our daytime estimates of fish abundance, which were derived from aggregated fish, were consistently and significantly lower.

Our findings lead us to conclude that acoustic estimates of fish abundance derived from ensonification of fishes that are densly schooled are likely to be regularly biased downward due to acoustic shadowing. Several potential solutions to this problem exist. One solution would be to survey only at times when fish are dispersed, or occur in loose schools. This solution is likely to be unobtainable for some species, but in many survey situations, such as the one we describe, it may be feasible to exploit day–night differences in schooling patterns to sample fish populations more accurately. Failing this, it may be necessary to consistently calibrate acoustic data derived from schooling fish by quantitative sampling. This may, however, be difficult to achieve, since many fish species are known to be difficult to sample quantitatively during daylight hours and when schooling (Blaxter and Parrish 1965; Woodhead 1966; Dembinski 1971; Leggett and Jones 1971; Northcote and Rundberg 1971; Morse 1989).

The biasing effects of fish aggregation on acoustic measurements can be established using the theoretical models of Lytle and Maxwell (1983). These theoretical models were developed to account for sound attenuation and interactions of echos when fish occur in high densities and multiple layers of fish are present in the acoustic wave. Burczynski et al. (1990), in an attempt to apply this model to acoustic data obtained from dense aggregations of fish contained in enclosures, found that while the model corrected fish estimates in the right direction, it failed to yield results consistent with the known fish density, the estimates being much too low when fish were ensonified with a downward oriented transducer. While this method can be tested and applied relatively easily in survey situations where a homogeneous aggregation of fish with constant acoustic signal is prevalent, difficulties arise when fish schools are patchy in their vertical or horizontal location and the survey vessel is moving along transects, as occurred in our daytime surveys (Fig. 5 and 6). Under these conditions the acoustic signal strength varies tremendously, ranging from very high values when a school is encountered to zero values when no schools are present (Fig. 6A). When calculating in situ fish densities from echo integration data, echos are typically averaged over large horizontal spatial intervals (Johannesson and Mitson 1983; Burczynski and Johnson 1986). In our case, we used 50-m intervals. However, in order to apply the Lytle and Maxwell (1983) models to correct acoustic densities obtained from in situ schools, echo integration data must be recorded from single schools that have been subdivided into thin depth layers. This greatly restricts the model's utility in large-scale surveys.

It is possible, however, to compute ratios of acoustic estimates obtained from comparatative surveys conducted at times when fish are dispersed and when they are aggregated in schools. Such ratios can then be applied as an "aggregation factor" in concert with the usual "scaling factor" in order to calibrate acoustic estimates of schooling fish. In our study the average "aggregation factor" required to compensate for the bias induced by day–night differences was 2.1 (SD 0.66; $n = 9$). Clearly, it would be desirable to derive more general empirical models with reliable measures of fish aggregation and school size with which to predict effects on echo signal strength. Toresen (1991) approached this problem for dense herring aggregations by calculating acoustic absorption in herring schools from observed losses in the bottom signal strength. He found that in the three schools he observed the "aggregation factor" ranged from 10 to 41% of the observed value. These values are lower than our estimates of 50%. Soria and Freon (1991) reported that acoustic estimates of fish abundance obtained at night from tropical oceanic regions were approximately twice those obtained during daylight hours. It is interesting that these diel differences are equal in direction and magnitude to those we observed, although the possibility that the differences Soria and Freon (1991) observed might be related to avoidance of the survey vessel during daylight cannot be dismissed (Soria and Freon 1991).

Clearly, many more such day–night studies will be required to effectively model the influence of fish aggregation and its associated acoustic shadowing on estimates of fish abundance. For the moment, however, it appears safe to conclude that estimates of fish abundance based on acoustic surveys conducted on schooling fishes should be considered regularly biased and that the magnitude of this bias could be less or more than 50%. Moreover, the results of our studies, together with those of Soria and Freon (1991), suggest that this bias may be avoided in cases where it is possible to take advantage of the natural behavior of fishes which alternate between aggregated and dispersed distributions and to time accoustic surveys to coincide with the interval during which they are dispersed.

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Alteration of Reproductive Steroids of Male Winter Flounder (*Pleuronectes americanus*) Chronically Exposed to Low Levels of Crude Oil in Sediments[1]

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Truscott, B., D. R. Idler, and G. L. Fletcher. 1992. Alteration of reproductive steroids of male winter flounder (*Pleuronectes americanus*) chronically exposed to low levels of crude oil in sediments. Can. J. Fish. Aquat. Sci. 49: 2190–2195.

When male winter flounder (*Pleuronectes americanus*) were held in seawater for 4 mo exposed to sand treated with five low levels of crude oil, there was a significant reduction in testosterone and 11-ketotesterone glucuronides in blood plasma. At the two higher levels of oil the concentrations of plasma glucuronides were similar but very significantly lower than in the controls or the three lower levels of oil. For both androgens the ratio of glucuronides to free steroids declined in a stepwise fashion. Free testosterone and 11-ketotestosterone plasma levels were not affected significantly by any concentration of oil in sediment. Liver weights as a percentage of body weight were significantly increased at the two highest levels of oil in the sediments, but neither body weights nor testes weights were altered by exposure to oil. It has been suggested that androgen glucuronides can function as pheromones in some fish and this is one potentially deleterious effect of exposure to oil.

Lorsque des sujets mâles de la plie rouge (*Pleuronectes americanus*) ont été gardés pendant 4 mo dans une eau de mer et exposés à du sable traité avec du pétrole brut à cinq faibles concentrations, il s'est produit une importante diminution de la concentration en testostérone et en glucuronides de 11-cétotestérone dans le plasma sanguin. Aux deux concentrations les plus élevées de brut, la concentration de glucuronides dans le plasma était semblable mais très significativement inférieure à la concentration des témoins ou à celle associée aux trois faibles concentrations de brut dans les sédiments. Dans le cas des deux composés androgènes, le rapport des glucuronides aux stéroïdes libres a diminué par paliers. La concentration de testostérone libre et de 11-cétostérone dans le plasma sanguin n'a pas varié de façon significative, peu importe la concentration de brut dans les sédiments. Le poids du foie en pourcentage de la masse corporelle a significativement diminué aux deux plus fortes concentrations de brut dans les sédiments, mais ni la masse corporelle ni la masse des organes génitaux n'a varié par suite de l'exposition au brut. Il a été proposé que les glucuronides androgènes peuvent agir comme phéromones chez certains poissons et que cette fonction serait éventuellement gravement atteinte par suite de l'exposition au pétrole.

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The winter flounder (*Pleuronectes americanus*) is a bottom-living fish often burrowing into and ingesting sediment while feeding. In locations where water temperatures are suitable, there is no extensive movement of flounder populations. Petroleum hydrocarbons can be incorporated into marine inshore sediments and have been shown to remain there for many years (Keizer et al. 1978) such that the flounder could be chronically exposed to oil residues. Although flounder off the coast of Newfoundland spawn in late May or early June, testicular growth and spermatogenesis begins in the early fall with gonads reaching maximal size in November. Under laboratory test conditions, chronic exposure of flounder to oiled sediments resulted in some inhibition of the autumnal growth of the testes (Fletcher et al. 1982).

In male flounder, the major steroids found in the circulating blood that are associated with sexual maturation are testosterone and its 11-oxygenated derivative, 17β-hydroxy-4-androstene-3,11-dione (11-ketotestosterone, 11-KT). Both androgens are also present in the peripheral blood as glucuronic acid conjugates. The plasmatic concentrations of free (unconjugated) androgens are maximal at spawning time in June and minimal in July when the testes are fully regressed and, except for a temporary increase in testosterone in September, the levels of both androgens are low (<10 ng/mL) in the autumn during testicular growth and development (Campbell et al. 1976). In the winter months (December through March), although the sperm are already activable (Burton and Idler 1984), androgen levels remain low (unpublished data). In several species of fish, the mature gonad has been identified as a major source of conjugated androgens (Grajcer and Idler 1963; Schoonen et al. 1989) or of the necessary glucuronyltransferase system (Kime 1982). There are no reports on seasonal variations in blood levels of the androgen glucuronides in flounder but, in both the fall and winter, the concentrations of testosterone and 11-KT glucuronides were determined to be less than 15 ng/mL (unpublished data).

During the spawning season, the total (i.e. free and conjugated) testosterone and 11-KT in the blood of male flounder were reported to be 200–300 and 500–800 ng/mL, respectively; exposure of these fish for 2 wk to water containing high levels of petroleum caused a significant reduction in these levels

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(Truscott et al. 1983). Comparison of the data obtained for total androgens in the control group in the 1983 study with levels of free androgen reported by Campbell et al. (1976) indicated that, in the mature male, the concentration of testosterone glucuronide was approximately five times greater than that of testosterone and that for 11-KT the ratio of glucuronide to free was approximately three. In the oil-treated group of fish, the levels of total androgens were more or less equal to the expected levels of free steroid, suggesting that the glucuronides had been preferentially affected by acute exposure to petroleum. This interpretation of the data was not confirmed experimentally but tests on a few samples suggested that the major effect of acute exposure of the flounder to oil was a decrease in the plasmatic androgen glucuronides.

The current study was undertaken to determine if chronic exposure to low levels of oil in sediments during the prespawning period would have the same effect as short-term, acute exposure, during spawning, on the reproductive hormones of male flounder and to determine if any effect is exhibited principally or only by the conjugated form of the hormones.

Materials and Methods

Winter flounder were collected by SCUBA divers from Conception Bay, Newfoundland, during December and January. They were maintained (before and during the experiment) in 300-L aquaria supplied with continuously flowing seawater under seasonally ambient conditions of water and temperature and photoperiod (Fletcher 1977).

Sand was obtained from the seafloor in an area populated by winter flounder. The sand was washed with seawater immediately after it was obtained and dried completely at room temperature (20–25°C). Venezuelan crude oil was thoroughly mixed into the dried sand at room temperature. Six experimental aquaria (300 L) were set up, each containing approximately 45 kg of sand. This amount gave a bottom layer of sand approximately 5 cm deep. The crude oil was added to the sand in aliquots of 5, 25, 50, 250, and 500 mL/45 kg sand. Sand containing no crude oil served as a control. Control and oiled sands in their respective aquaria were washed thoroughly with cold seawater (~1°C) (8–12 L/min) for 7 d. Each day, the sand was mixed into the water column to ensure adequate washing. After 7 d, there was no visible oil slick on the surface of the water.

Male winter flounder were added to the experimental aquaria (February 16) 8 d after the oiled sediments; the five experimental groups were designated E5, E25, E50, E250, and E500. Winter flounder do not normally eat during winter (Fletcher and King 1978), so the fish were not fed during the experimental period. Water temperatures ranged from −1°C in February to +5°C in June. At the end of the exposure period (June 18–27), flounder were removed from the aquaria and bled within 1 min of capture. In order to avoid unnecessary stress, care was taken to avoid chasing the flounder around the aquaria (Fletcher 1975). Blood samples (1.5–2 mL) were obtained from a caudal blood vessel using plastic 3-mL syringes equipped with 23-gauge needles and heparinized (sodium-heparin) Vacutainers (Becton-Dickinson). The cells were centrifuged (~400 × *g*) from the blood and the plasma frozen and stored at −20°C until analyzed.

Total body lengths and body and organ weights were recorded for each fish. The flounder used in the experiments described in this paper were part of a larger group of flounder which were examined for a variety of biological and biochemical changes affected by chronic exposure to hydrocarbons in sediment (Payne et al. 1988).

Analytical

Plasma steroid levels were measured by radioimmunoassay. A specific antiserum, described by Idler and Ng (1979), was used to measure 11-KT. Rabbits previously injected with the 3-0-carboxymethyl oxime derivative of testosterone conjugated with bovine serum albumin (Steraloids, Inc., Wilton, NH) provided an antiserum to testosterone which, when tested against the major androgens and their metabolites, showed cross-reactions only with 17β-hydroxy-5α-androstan-3-one (34%), 17β-hydroxy-5β-androstan-3-one (6%), and 5α-androstane-3β,17β-diol (3%). Cross-reactivity was calculated at the 50% displacement level as described by Abraham (1975). Tritiated steroids were used in the assays as both label and recovery tracer. [1,2,6,7-^{3}H]Testosterone was purchased from New England Nuclear, Boston, MA. Tritiated 11-KT was synthesized from [1,2-^{3}H]hydrocortisone as outlined by Truscott (1981). The glucuronic acid conjugate of [^{3}H]testosterone was made biosynthetically. A microsomal fraction prepared from mature rainbow trout (*Oncorhynchus mykiss*) testes was incubated under conditions adapted from Lucier (1974) with [1,2,6,7-^{3}H]testosterone in the presence of the ammonium salt of uridine 5′-diphosphoglucuronic acid (UDPGA). After removal of nonconjugated testosterone from the incubation medium by extraction with dichloromethane, testosterone glucuronide was extracted at pH 2 into ethyl acetate and then purified by paper chromatography in the solvent system *n*-butyl acetate – toluene – 10% acetic acid – methanol – *n*-butanol (50:40:50:50:40). The position of the radioactive testosterone glucuronide on the paper chromatogram was determined by radioscan. A mixture of ethanol and 0.1 M aqueous acetic acid (9:1, v/v) was used to elute the glucuronide from the paper. The identity and purity of [^{3}H]testosterone glucuronide was established by the addition of [^{14}C]testosterone (New England Nuclear) to an aliquot of the paper eluate to give a known isotope ratio, hydrolysis with β-glucuronidase EC 3.2.1.31 from bovine liver (Sigma, type B10) as described below, and extraction of the free steroid. The isotope ratio of the extract remained constant through the hydrolysis and subsequent chromatography and recrystallization three times with authentic testosterone.

Tracer amounts of [^{3}H]testosterone, [^{3}H]11-KT, and [^{3}H]testosterone glucuronide (~1500 dpm), each in 100 μL of saline, were added to plasma samples (100 μL) previously diluted with 200 μL of saline. After equilibration of the samples overnight at 4°C, the free steroids were extracted twice with 4 mL of diethyl ether. The ether extracts were recovered from the aqueous layer by immersion of the tubes in powdered dry ice and decantation of the ether. The aqueous layer was mixed with an equal volume of 0.2 M sodium acetate buffer, pH 4.6, containing 1500 Sigma units β-glucuronidase/volume and incubated at 37°C for 24 h. A solution of [^{3}H]11-KT in saline, 100 μL containing approximately 1500 dpm, was added to each sample and the incubation continued for a further 16 h. The steroids released by the β-glucuronidase were recovered by ether extraction as before. Ether extracts were evaporated to dryness under nitrogen. Testosterone and 11-KT were isolated from all extracts by paper chromatography as described by Truscott et al. (1983). Areas of the paper strips containing 11-KT and testosterone, as well as appropriate areas of blank strips, were eluted with 5 mL of ethanol. The ethanolic extract was filtered through glass fibre discs to remove any paper fibres and then evaporated to dryness under nitrogen. Residues were dissolved in 1.0 mL of assay buffer. An aliquot (200 μL) was removed for determination of procedural losses and a second aliquot (50 μL) was used in a preliminary radioimmunoassay to estimate suitable dilutions for accurate measurement of each steroid. For final analyses, all samples were set up in the assay at three levels, in duplicate. Procedures, including buffer composition, separation of free from antibody-bound steroid with dextran–charcoal, and setting up standard curves and samples for assay, followed those outlined by Simpson and Wright (1977).

The recovery of testosterone and 11-KT averaged 62 ± 1.7 (SE)% and 68 ± 1.3%, respectively; for the glucuronides, the values were 55 ± 3.0 and 71 ± 1.1%. The value for testosterone glucuronide was a true measure of procedural losses, including the efficacy of the β-glucuronidase, since radioactive testosterone glucuronide was used as a tracer. For 11-KT glucuronide, the recovery was a measure of the losses incurred through extraction only and assumes complete hydrolysis such that the quantities of 11-KT glucuronide reported are minimal. Under the standardized conditions of the assay, the minimum level of measurement for both steroids was 1.5 ng/mL serum. Blank values were less than the level of detection. The reproducibility of the steroid measurements was assessed by including, through the total procedure, a control plasma sample from mature male flounder: the values ($N = 10$) obtained were 19 ng/mL (coefficient of variation, CV 10%) for testosterone, 380 ng/mL (CV 10%) for testosterone glucuronide, 220 ng/mL (CV 6%) for 11-KT, and 550 ng/mL (CV 10%) for 11-KT glucuronide.

Results

Body weights and testes weights (percentage of body weight) of the flounder exposed to five levels of oil in sediment did not differ significantly among the experimental groups or the control group (no oil in sediment); however, liver weights (percentage of body weight) were significantly greater in flounder exposed to the higher levels of oil (E250 and E500) (Table 1).

Free testosterone and 11-KT levels were not affected significantly by any level of oil tested (Table 1). At the lowest level of oil (E5), both androgen glucuronides were significantly less than in the control fish but similar to those in fish held at levels of E25 and E50. At the higher levels of oil (E250 and E500), the concentration of glucuronides was similar but significantly lower than in control flounder and groups E5, E25, and E50. For both androgens, the ratio of the glucuronides to the free compound declined in a stepwise fashion.

Discussion

Hydrocarbon analysis of the crude petroleum used in these experiments and of the residual oil in the sediments was reported in tables 1 and 2 of Payne et al. (1988). Polycyclic aromatic hydrocarbons (PAH) are of major concern because of their cytotoxic properties. The crude petroleum contained approximately 1.5% PAH with napthalenes as the major component (65%). Analysis of the sediments indicated that the napthalenes were essentially removed by the initial washing of the sand (i.e. before the flounder were placed in the tanks, except in tank E500 where measurable amounts remained at the end of the experiment). Weathering of the higher molecular weight, three-ring aromatics occurred but to a lesser extent and, at the higher levels (E250 and E500), the residual amounts were similar. McCain et al. (1978) showed that the concentration of extractable hydrocarbons from oil–sediment mixtures in aquaria decreased rapidly during the first month but, subsequently, the decrease was slow over a 4-mo period to give a relatively stable concentration.

Gonad weight relative to body weight was not affected at any of the five levels of oil. This result is in agreement with an earlier study, using a higher concentration of oil, when the exposure period extended from February to June (Fletcher et al. 1982) and not entirely unexpected, since testicular growth and spermatogenesis in this species would be complete before the exposure to oil (Fletcher and King 1978; Burton and Idler 1984). The effect of petroleum on gonadal growth in male flounder depends on the stage of development: testicular growth was significantly reduced in male flounder exposed to oiled sediments from July to November (Fletcher et al. 1982). The marine cunner (*Tautogolabrus adspersus*), when exposed to what could be considered maximum amounts of crude oil for 6 mo, showed no histopathological changes in the testes but the gonadosomatic index was reduced (Payne et al. 1978). Gonad development and spermatogenesis in males of several demersal fishes collected near petroleum production platforms in the Gulf of Mexico correlated with specimens captured in control areas and there was no evidence of an adverse effect by petroleum production activity on gonad morphology (Stott et al. 1980). However, these authors did not record actual or estimated levels of petroleum in the sediments at the collection sites. Testicular maturation was reported to be accelerated in the starry flounder (*Platichthys stellatus*) by exposure to petroleum but there were no other obvious changes in testicular structure (Whipple et al. 1978). However, the starry flounder were exposed to water-soluble fractions rather than the higher molecular weight compounds present in the sediment under our conditions.

The blood plasma levels of free testosterone and 11-KT reported here for the control samples, 23 and 224 ng/mL, respectively, compare reasonably well with the values, 50 and 180 ng/mL, reported previously for mature male flounder in June (Campbell et al. 1976). Free testosterone was not affected by exposure to any level of oil in the sediments. At the higher concentrations of oil (E250 and E500), there was a trend to lower values of 11-KT but at no level of oil was there a significant effect. The gonadal enzymes required for the biosynthesis of 11-KT, 11β-hydroxylase/dehydrogenase, have been shown to be sensitive to some environmental pollutants. Freeman et al. (1980) suggested that examination of steroid hormone metabolism could serve to assess the effects of sublethal pollutants on marine animals and reported that organochlorine pesticides and heavy metals, for example, influence the pattern of steroidogenesis both in the gonad and interrenal of teleosts. Very low levels of polychlorinated biphenyl (PCB) in the diet of cod resulted in an increase, relative to controls, in the testicular production in vitro of testosterone and 11-KT but, at higher levels, the production of 11-KT was inhibited completely. Androgens in the blood of these fish did not increase during sexual maturation as demonstrated in the control fish. It should be noted that androgen glucuronides were not measured in any of these past studies.

The most dramatic effect of oil on our flounder was the decline in androgen glucuronides in the peripheral blood. The concentration of both testosterone and 11-KT glucuronides in the flounder group E5 held in sediments containing the least amount of oil residue was approximately 60% of the control values and, in fish held at the two highest levels of oil (E250 and E500), it was 20% or less. The effect of the long-term exposure to the most contaminated sediment was quantitatively similar to that obtained when spawning male flounder were held for 2 wk in tanks containing excess crude oil (Truscott et al. 1983). Because changes in total (free and glucuronide) androgen concentration were measured in the short-term experiment,

TABLE 1. Effects of oil-treated sediments on plasma androgen steroid levels in winter flounder. All values expressed as means ± 1 standard error. Numerals in parentheses represent the number of analyses. Exposure groups E5, E25, E50, E250, and E500 were exposed to 5, 25, 50, 250, and 500 mL oil/45 kg dried sediment, respectively. Comparisons between treatments were carried out by a one-way analysis of variance followed by Duncan's multiple range test. Groups with the same letter do not differ significantly ($P > 0.05$).

		Oil-exposed				
	Control	E5	E25	E50	E250	E500
Body weight (g)	239 ±18.4 (11) A	260 ±29.6 (12) A	236 ±19.9 (12) A	220 ±14.3 (13) A	212 ±15.8 (13) A	240 ±24.8 (12) A
Liver (% of body weight)	0.68 ±0.02 (11) A	0.74 ±0.03 (12) A	0.74 ±0.03 (12) A	0.78 ±0.03 (13) A	1.08 ±0.04 (13) B	1.10 ±0.05 (12) B
Testes (% of body weight)	7.61 ±0.40 (11) A	7.56 ±0.44 (12) A	7.96 ±0.50 (12) A	8.12 ±0.52 (13) A	8.65 ±0.73 (13) A	8.26 ±0.54 (12) A
Testosterone, free (T) (ng/mL)	22.7 ±2.45 (11) A	21.0 ±2.37 (12) A	23.4 ±2.80 (12) A	19.4 ±1.37 (13) A	29.0 ±5.18 (13) A	23.7 ±4.98 (12) A
Testosterone glucuronide (TG) (ng/mL)	205 ±39 (11) A	121 ±21 (12) B	121 ±16 (12) B	109 ±17 (13) B	45.2 ±10.2 (13) C	36.8 ±8.67 (12) C
Ratio TG/T	9.14 ±1.24 (11) A	5.91 ±0.71 (12) B	5.41 ±0.92 (12) B	5.30 ±0.59 (13) B	2.32 ±0.57 (13) C	1.87 ±0.36 (12) C
11-Ketotestosterone, free (11-KT (ng/mL))	224 ±23 (11) A	185 ±32 (12) A	217 ±25 (12) A	235 ±36 (13) A	173 ±41 (13) A	133 ±34 (12) A
11-Ketotestosterone glucuronide (11-KTG) (ng/mL)	360 ±73 (11) A	191 ±42 (12) B	237 ±53 (12) B	184 ±35 (13) B	51 ±14 (13) C	50 ±18 (12) C
Ratio 11-KTG/11-KT	1.49 ±0.2 (11) A	0.98 ±0.09 (12) B	1.00 ±0.16 (12) B	0.73 ±0.07 (13) B	0.37 ±2.06 (13) C	0.33 ±0.07 (12) C

our study strongly suggests that acute exposure to high levels of oil also preferentially affected the level of conjugated steroid.

A decrease in the concentration of the conjugated androgens in the peripheral plasma of the oil-treated flounder could result from inhibition of their gonadal synthesis or enhancement of their metabolism and clearance. Because the concentration of the free androgens was not affected at any level of oil exposure, the most obvious explanation of the results is an inhibition of glucuronide production. Although there is extensive literature on UDP-glucuronyltransferase systems, particularly in mammalian liver, many questions remain concerning multiple forms and related specificities, regulatory properties, and species differences (Dutton 1966, 1975, 1980).

Information on teleost gonadal UDP-glucuronyltransferase and control of production of steroid glucuronides in fish is so limited that one can only speculate on the basic cause of the decline in peripheral blood levels of androgen glucuronides in exposed fish. The necessary enzyme system is present in the testes of several species of teleost (Kime 1982) and it is located in the microsomal fraction of trout gonad homogenates (see Materials and Methods, this paper) but may also be present in the nuclear fraction (unpublished data). Manning and Kime (1985) reported that glucuronyltransferase activity was seasonal, being high during full sexual maturity and declining in the regressed testes of trout. These gonadal enzymes are stimulated in vitro by increases in temperature within certain limits, and it has been suggested that the conversion of androgens to their glucuronides could serve to control active androgen levels until water temperatures are suitable for spawning; experiments in vivo did not substantiate this hypothesis (Kime 1982). It should be noted that hepatic UDP-glucuronyltransferase in trout also shows a noncompensation pattern to temperature (Hänninen et al. 1984). However, temperature effects on the synthesis of glucuronides in the oil-treated flounder were not a factor, since both the control and experimental animals were maintained under identical conditions.

UDP-glucuronyltransferase activity depends on UDPGA being available. Testicular tissue of mature teleosts must have some UDPGA available, since in vitro exogenous steroids, to a limited extent, can be converted to their glucuronic acid conjugates (Hews and Kime 1978; Kime 1982). Also, UDP-glucuronyltransferase, the enzyme necessary for the synthesis of UDPGA by oxidation of UDP-glucose, was demonstrated to occur in the interstitial cells of testes of a teleost (van den Hurk et al. 1987). The conversion of glycogen through glucose-1-phosphate and UDP-glucose to UDPGA in mammalian liver is well documented (Dutton 1966) but, to our knowledge, there have been no studies on the source of UDPGA in the teleost gonad. There was no effect on glucose content of muscle or liver in any of the fish exposed to oil in our experiment although glycogen levels in the liver, but not muscle, were higher in the flounder in groups E250 and E500; glucose levels in blood were not measured (Payne et al. 1988).

Xenobiotics have been reported to cause a marked reduction in the concentration of UDPGA in mammalian hepatic tissue (Geregus et al. 1983). Quantification of UDPGA in the testes by a direct method such as high-pressure liquid chromatography (Schiller et al. 1982) and thus not dependent on the activity of the UDP-glucuronyltransferase present could determine if the transferase and/or its cosubstrate UDPGA were affected by exposure of the fish to petroleum.

In teleosts, steroid hormones and their metabolites are excreted into the bile and urine as water-soluble conjugates and no ''free'' steroids are recovered from these fluids. In the mature flounder, 20–50% of an intraarterially injected dose of [^{3}H]testosterone was recovered in the bile as the glucuronic acid conjugates of testosterone, 17β-hydroxy-5β-androstan-3-one (5β-dihydrotestosterone) and 5β-androstane-3α,17β-diol; the three compounds were present in more or less equal quantities (Truscott 1983). The metabolism of testosterone and testosterone glucuronide in mature male flounder was compared by the separate injection of radioactive forms of each compound: radioactive glucuronides were recovered from urine as well as bile and the same metabolites were identified from each precursor in both fluids; the only differences noted were a slower clearance and poorer recovery of total radioactivity in the bile and urine of the fish injected with [^{3}H]testosterone glucuronide (unpublished data). The results of both experiments strongly suggest that the flounder can excrete the water-soluble glucuronides from the blood by means other than the bile and urine — perhaps gills. It has been shown that the gills and intestine of some species have UDP-glucuronyltransferase activity as measured by the biotransformation of 4-nitrophenol (Lindström-Sëppa et al. 1981) but it was not determined if these organs also play an excretory role by conjugation of the free form. Förlin and Haux (1985) showed that, in trout, hepatic UDP-glucuronyltransferase activity towards estradiol was significantly increased by exposure of the fish to β-naphtho flavone which, like petroleum hydrocarbons, is an inducer of cyctochrome P-450 monooxygenases (Payne and Fancey. 1982). Estradiol was recovered in the bile as estradiol-derived glucuronides but the elevated biliary levels of radioactivity in the treated fish were not accompanied by a change in radioactivity in the blood, i.e. the clearance from the blood was not limited by hepatic metabolism and biliary excretion. In the present study, bile samples were not collected but in the previous work where mature male flounder were exposed to maximal levels of water-accommodated petroleum for 2 wk (Truscott et al. 1983), biliary levels of total androgens (free and conjugated) were not affected even though blood levels were decreased significantly; in the salmon, both blood and bile levels of total androgens were reduced in the oil-treated fish. An increase in UDP-glucuronyltransferase activity in liver or other tissues would be expected to result in lower levels of free testosterone and 11-KT in the peripheral plasma of the oil-treated fish but such was not the case.

A decline in plasma levels of the glucuronides of testosterone and 11-KT would occur if the hepatic metabolism of the two androgens were more extensive in the oil-treated fish. As noted above, testosterone is metabolized in flounder to produce approximately equal amounts of the glucuronides of testosterone, 5β-dihydrotestosterone and 5β-androstane-3α,17β-diol. If, because of exposure to petroleum, more of the latter two metabolites were produced, then our assay for testosterone glucuronide would show a reduction in its level. This explanation assumes that at least a part of the hepatic metabolites reenter the peripheral circulation. To our knowledge, there have not been any studies on the effect of enzyme inducers on the steroid 4-ene-5β-reductase and 3α-hydroxy-steroid dehydrogenase enzyme systems of fish liver. A similar shift in testosterone metabolism conceivably could occur in the gonad: the glucuronides of 5β-androstane-3α,17β-diol and the corresponding metabolite of 11-KT were shown to be products of the gonad of *Tilapia* (Kime and Hyder 1983). Whether 5β-reduced testosterone derivatives are normal products of the flounder testes is not known, nor are there any reports of their occurrence in the peripheral blood. However, if exposure to petroleum did stimulate the appropriate enzyme systems in the gonad, the levels of testosterone glucuronide would decrease, especially since, in mammals at least, the glucuronide is a better substrate for the reductase than is the free steroid. At present, there is no practical assay such as radioimmunoassay for the 5β-reduced androgens but such an assay could be used to determine if hydrocarbon exposure affected the metabolism of the gonadal androgens in fish.

Exposure of salmon to maximal amounts of petroleum for a few weeks did not affect the viability of sperm as evidenced by their capacity to fertilize eggs (Truscott et al. 1983). Fertility tests were not made in the current study on flounder but there was no evidence of any deleterious effect on sperm production although the fish were exposed to oiled sediments during the period between spermatogenesis and maturation (Burton and Idler 1984).

In summary, long-term exposure to extremely low levels of crude petroleum in sediments caused a significant dose-dependent decrease in levels of testosterone and 11-KT glucuronides in the blood of mature male flounder, probably as a result of inhibition of their formation in the gonad. The physiological consequences are difficult to predict because the role of the androgen glucuronides in teleost reproduction has not been established fully, although it is possible that they may act as pheromones during spawning (Columbo et al. 1982).

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Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation

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Interspecific patterns of fish life histories were evaluated in relation to several theoretical models of life-history evolution. Data were gathered for 216 North American fish species (57 families) to explore relationships among variables and to ordinate species. Multivariate tests, performed on freshwater, marine, and combined data matrices, repeatedly identified a gradient associating later-maturing fishes with higher fecundity, small eggs, and few bouts of reproduction during a short spawning season and the opposite suite of traits with small fishes. A second strong gradient indicated positive associations between parental care, egg size, and extended breeding seasons. Phylogeny affected each variable, and some higher taxonomic groupings were associated with particular life-history strategies. High-fecundity characteristics tended to be associated with large species ranges in the marine environment. Age at maturation, adult growth rate, life span, and egg size positively correlated with anadromy. Parental care was inversely correlated with median latitude. A trilateral continuum based on essential trade-offs among three demographic variables predicts many of the correlations among life-history traits. This framework has implications for predicting population responses to diverse natural and anthropogenic disturbances and provides a basis for comparing responses of different species to the same disturbance.

Les caractéristiques du cycle biologique communes à plusieurs espèces de poissons ont été évaluées par rapport à plusieurs modèles théoriques de l'évolution à l'intérieur du cycle biologique. On a recueilli des données sur 216 espèces nord-américaines de poissons (57 familles) afin d'explorer les rapports entre différentes variables et afin de classer les espèces. Des tests multivariés, faits sur des matrices correspondant aux eaux douces, aux eaux de mer et aux deux, ont régulièrement fait ressortir un gradient qui associe les poissons à maturation lente à une fertilité élevée, à la petitesse des oeufs et au nombre restreint de périodes d'activité sexuelle au cours d'une brève saison de fraie, et qui associe les traits opposés aux poissons de petite taille. Un deuxième gradient marqué a indiqué des associations positives entre les soins des parents, la grosseur des oeufs et l'existence de saisons de fraie prolongées. La phylogénie a des effets sur chacune des variables, et certains groupes taxonomiques supérieurs sont associés à des stratégies particulières du cycle biologique. Il tendait à exister un rapport entre la fertilité élevée et l'aire de distribution des grosses espèces en milieu marin. L'âge à maturité, la vitesse de croissance des adultes, la durée de vie et la grosseur des oeufs étaient tous en corrélation positive avec l'anadromie. Les soins des parents étaient en corrélation inverse avec la latitude médiane. Un ensemble trilatéral de données fondées sur des compromis essentiels entre trois variables démographiques, permet de prédire beaucoup de corrélations avec les caractéristiques du cycle biologique. Ce cadre d'examen est utile à la prévision des réponses de populations à différentes perturbations naturelles et d'origine anthropique, et il procure la base pour la comparaison des réponses de différentes espèces à une même perturbation.

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Balon (1975) listed the requirements for a comparative framework useful for predicting the response of fish populations to different kinds of environments and disturbances. Such a framework should contain few categories and allow researchers "to build from bits and pieces of available information about reproductive strategies" (Balon 1975). Moreover, it should group similar species irrespective of phylogenetic origin. In other words, adaptive convergences should be stressed over phylogentic affiliations. Balon's (1975; Balon et al. 1977) reproductive guild framework was based on the premise that environmental requirements and adaptations of early life stages are likely to account for a large amount of the variance in densities and geographical distributions of fish populations. Reproductive guilds permit researchers and resource managers to identify common ecological features and problems in different geographical locations involving different fish faunas.

Because it is qualitative and emphasizes the physiological ecology of early life stages, the reproductive guild concept is limited in its application to many practical problems. Much of population biology and fisheries science is founded in mathematical formulations, and a framework based on developmental physiology does not easily yield quantitative predictions. Hence, a general, yet quantitative comparative framework that could interface with both qualitative schemes, like reproductive guilds, and quantitative population models is desirable. To provide a further step toward a conceptual framework of fish ecological strategies, we examine patterns of life-history variation among North American fresh water and marine fishes and evaluate gradients of variation in relation to several earlier models of life-history evolution.

Because life-history traits are also the fundamental determinants of population performance, the investigation of life-strategies is central to both theoretical ecology and resource management. Life-history theory deals with constraints among demographic variables and traits associated with reproduction and the manner in which these constraints, or trade-offs, shape strategies for dealing with different kinds of environments. Life-history trade-offs may have a primarily physiological basis (e.g. clutch size and investment per offspring; Smith and Fretwell 1974), a demographic basis (e.g. intrinsic rate of increase and mean generation time; Birch 1948; Smith 1954), an ecological basis (e.g. provision of parental care and clutch size; Sargent et al. 1987; Nussbaum and Schultz 1989), or a phylogenetic basis (Gotelli and Pyron 1991). Of course, organisms consist of complex suites of life-history traits, so that genetic correlations between coevolved traits exhibiting a strong trade-off can indirectly result in correlations with other traits (Pease and Bull 1988). For example, Roff (1981) reevaluated Murphy's (1968) findings for clupeid life histories and concluded that variation in reproductive life span could be explained by its correlation with age at maturity, rather than as a direct evolutionary response to variation in reproductive success.

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Insights into the evolutionary response of life-history parameters to different environmental conditions and spatiotemporal changes usually come from two approaches: theoretical models of life-history evolution (e.g. Cole 1954; Cohen 1967; Goodman 1974; Schaffer 1974; Green and Painter 1975; Boyce 1979; Roff 1984; Sibly and Calow 1985, 1986) and analyses of empirical patterns (e.g. Kawasaki 1980; Stearns 1983; Dunham and Miles 1985; Roff 1988; Winemiller 1989; Paine 1990). Both of these approaches have relied, to a large degree, on the *r–K* continuum (Pianka 1970) or similar unidimensional schemes (e.g. bet-hedging (Murphy 1968) and iteroparity–semelparity gradients (Cole 1954; Schaffer 1974)) as the basis for comparing alternative life-history strategies. Triangular continua containing three endpoint strategies (*r*-, *K*-, and stress- or adversity-resistance) have been adopted to interpret patterns and consequences of observed life-history variation in plants and insects (Grime 1977, 1979; Southwood 1977, 1988; Greenslade 1983). Studying fishes in very different environments, Kawasaki (1980, 1983), Baltz (1984), and Winemiller (1989; Winemiller and Taphorn 1989) independently identified three similar strategies as endpoints of a triangular continuum. Following Winemiller (1992), these can be classified as (1) small, rapidly maturing, short lived fishes (opportunistic strategists), (2) larger, highly fecund fishes with longer life spans (periodic strategists), and (3) fishes of intermediate size that often exhibit parental care and produce fewer but larger offspring (equilibrium strategists).

Here, we further evaluate the trilateral continuum model of fish life-history strategies by analyzing data from 216 North American freshwater and marine fish species. Even though many North American species are not included here, the breadth and evenness of phylogenetic coverage should be sufficient to identify major axes of life-history variation and to ordinate species into a framework of basic ecological and demographic strategies. We adopt broad interspecific comparisons under the assumption that consistent intercorrelations among life-history features across widely divergent taxa are likely to reveal both fundamental constraints and adaptive responses to environmental conditions. Life-history traits and strategies are then examined with respect to phylogeny, and observed patterns are evaluated in reference to several models of life-history evolution and population regulation. Finally, we argue that greater understanding of population regulation in fisheries can be achieved by contrasting alternative life-history strategies in relation to different scales of variation in resources and sources of mortality.

Materials and Methods

Life-History Data Set[2]

Estimates of fish life-history traits were obtained from literature sources that summarize large amounts of quantitative data for individual species (e.g. Carlander 1969, 1977; Hart 1973; and synopses of biological data published by Food and Agriculture Organization, Rome). In some instances, we consulted the original studies cited in the species synopses to allow better judgement of the method of estimation and reliability of data. Most fish species exhibit considerable interdemic variation in life-history traits over their geographical ranges. Therefore, we determined the average or modal value of traits by using data from populations located near the center of species' ranges. For example, if a freshwater species ranged from central Canada to the Tennesse River, we sought studies conducted near the latitudes of the Great Lakes. When limited data were available near the center of the range, we sought estimates from peripheral populations in an incremental fashion (working outward from the center of the range). When no reliable data were found for a given trait, that cell in the species by life-history trait matrix was left blank and all calculations calling for the trait eliminated the species from the analysis. Whenever maturation and growth data were reported for the sexes separately, we used the estimates for females. In some instances, total lengths were calculated from standard lengths or fork lengths using published conversion equations. Because no conversion equations were available for North American cavefishes (Amblyopsidae), we estimated conversion ratios from measurements of photographs.

Data were obtained for the following 16 life-history traits.

(1) Age at maturation — the mean age at maturation in years, or when estimates were in summarized form, the modal age of maturation.

(2) Length at maturation — the modal length at maturation in millimetres total length (TL), or if not reported, either the median or minimum length at maturation.

(3) Maximum length — the maximum length reported in millimetres TL.

(4) Longevity — maximum age in years.

(5) Maximum clutch size — the largest batch fecundity reported.

(6) Mean clutch size — the mean batch fecundity for a local population, i.e.data from a specific location or ecosystem, calculated as

$$(1)\quad E = \frac{\sum_{i=1}^{n} N_i F_i}{\sum_{i=1}^{n} N_i}$$

where E is the mean clutch, N_i is the number of individuals in age or size class i, F_i is the number of mature eggs per clutch, and n is the number of age or size classes in the population.

(7) Egg size — the mean diameter of mature (fully yolked) ovrian oocytes (to nearest 0.01 mm).

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[2] A database listing our principal literature sources, life history traits, and numerical estimates is available, for a nominal fee, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2, Canada.

(8) Range of egg sizes — the range of diameters for mature ovarian oocytes reported for a local population (0.01 mm).

(9) Duration of spawning season — number of days that spawning or early larvae were reported.

(10) Number of spawning bouts per year — the mean number of times an individual female was reported to spawn during a year. Because multiple spawning bouts are difficult to document in wild fishes, many of the estimates used in this analysis are probably underestimates. Several recent studies of small cyprinids and percids indicate that multiple clutches may be common in small fishes having small clutches (e.g. Heins and Rabito 1986; Heins and Baker 1988; James et al. 1991). When two fairly distinctive size classes of ova were reported in mature ovaries and other evidence was consistent with a hypothesis of repeat spawning, we recorded the species as having two bouts per year. Following Hubbs (1985), we used an average interbrood interval of 10 d for estimates of spawning bouts for several darters (*Etheostoma*, Percidae) that exhibited strong evidence of multiple clutches.

(11) Parental care — following Winemiller (1989), quantified as Σx_i for $i = 1$ to 3 ($x_1 = 0$ if no special placement of zygotes, 1 if zygotes are placed in a special habitat (e.g. scattered on vegetation, or buried in gravel), and 2 if both zygotes and larvae are maintained in a nest; $x_2 = 0$ if no parental protection of zygotes or larvae, 1 if a brief period of protection by one sex (<1 mo), 2 if a long period of protection by one sex (>1 mo) or brief care by both sexes, and 4 if lengthy protection by both sexes; and $x_3 = 0$ if no nutritional contribution to larvae (yolk sac material is not considered here), 2 if brief period of nutritional contribution to larvae (= brief gestation (<1 mo) with nutritional contribution in viviparous forms), 4 if long period of nutritional contribution to larvae or embryos (= long gestation (1–2 mo) with nutritional contribution), or 8 if extremely long gestation (>2 mo). We reason that, in terms of benefits received by offspring, gestation with nutritional contribution is approximately equivalent to biparental brood guarding during an equivalent time period. Parental care values (Σx_i) ranged between 0 (no care) and 8 (long gestation in some embiotocid fishes) in the North American fish data set.

(12) Time to hatch — the mean time to hatch within the range of values for average midseason temperatures, or when not reported, the mean, modal, or midrange time to hatch at the highest temperature reported within a reasonable range (relative to local ambient temperatures) for a given locality.

(13) Larval growth rate — mean increment in millimetres TL during the first month following hatching. We subtracted the length of larvae at hatching from the mean length attained after the first month. For the few species with larval stage duration <1 mo, we converted mean daily growth rates to mean increments for 30 d.

(14) Young of the year (YOY) growth rate — mean increment in millimetres TL during the first year following hatching or independent life for viviparous fishes. We subtracted the length of larvae at hatching from the mean or modal length attained after the first growing season.

(15) Adult growth rate — mean increment in millimetres TL per year of life over an average adult life span (in this case, data were not weighted by sample size of age cohorts).

(16) Fractional adult growth — mean fraction of millimetres TL gained per year in a normal adult life span, calculated from

$$G = \frac{\sum_{i=2}^{n} I_i/L_{i-1}}{n}$$

where I_i is the annual length gain for adults in age class i, L_i is TL for an adult entering age class i, and n is the number of adult age classes.

Within local populations and size classes, individual fish exhibit considerable variation in life-history traits. Our analysis assumes that measures of central tendency for populations near the center of their species distributions allow the investigation of relationships among life-history variables within a broad inter-specific context.

Phylogeny and Ecological Data Set

Phylogeny of North American fishes follows Lee et al. (1980) for freshwater fishes and Nelson (1984) for marine fishes. We coded family and order as categorical variables for statistical analyses of phylogenetic influences on life-history traits. Each species was classified as either freshwater or marine depending on where the greatest fraction of the life cycle occurred. Because the majority of the estuarine populations extend into other coastal marine habitats, estuarine fishes were included in the marine category. We obtained data for marine populations of *Oncorhynchus mykiss* (steelhead), *Menidia beryllina* (inland silverside), and *Gasterosteus aculeatus* (threespine stickleback) and data for a landlocked freshwater population of *Oncorhynchus nerka kennerlyi* (kokanee salmon).

For each species, the ecological data set consisted of variables characterizing its geographical range, general habitat, and general ecological niche. We recorded the midrange latitude and total range in latitude for each species based on range maps or verbal accounts of species' ranges. Each species was classified as either benthic (1), epibenthic (2), or pelagic (3) based on accounts of the normal depth distribution of adult fishes. The basic adult habitat was classified as either caves or springs (0), small cold-water streams (1), small warmwater streams (2), river channels (3), river backwaters and lakes (4), estuaries (5), marine benthic (6), or marine pelagic (7). Fishes that are common in two or more categories or occupy intermediate habitats were assigned fractional values (e.g. habitat = 2.5 for *Ictiobus bubalus* (smallmouth buffalo) which commonly occurs in both rivers and lakes). Based on summarized diet information for adults, trophic status was classified as either detritivore/herbivore (1), omnivore (2), invertebrate-feeder (3), or piscivore (4). Fishes that consume large quantities of both invertebrates and fishes formed a fifth intermediate category (e.g. trophic status = 3.5 for *Micropterus dolomieu* (smallmouth bass)). The relative migratory behavior of each species was classified under the headings anadromous (1), sedentary (0), and catadromous (−1). Fishes exhibiting spawning runs from lakes into rivers or from rivers into affluent tributaries (potamodromy) were classified as 0.5, and fishes exhibiting spawning migrations from nearshore to offshore were classified as −0.5.

Data Analysis and Comparisons

Analyses based on broad interspecific comparisons yield patterns that have resulted from many generations and thousands of years of evolution. As a consequence, comparisons involving many taxa and large phylogenetic breadth should contain fewer idiosyncracies due to genetic correlations carried along within a particular phylogenetic lineage (= phylogenetic constraints). If divergent lineages are not given fairly equivalent representation, taxonomic bias can enter into interspecific comparisons (Pagel and Harvey 1988). Some have even argued against the use of species in comparisons (e.g., Ridly 1989).

In essence, the comparative approach requires that a pattern be repeated consistently within a variety of taxa (i.e. conservation or convergence of pattern), or the effect of phylogeny be held constant (or adjusted for statistically), if hypotheses of adaptation are to be tested. To maximize the likelihood that emergent patterns reflect adaption, we examined life-history patterns based on a variety of different combinations of life-history traits and various ecological and phylogenetic subsets of the overall data set.

Because some distributions of raw life-history traits were log-normal, data were ln-transformed for parametric statistical tests. All statistics were calculated using SAS (SAS Institute Inc. 1987). Univariate comparisons between various subsets of the data set used either *t*-tests (two-sample, two-tailed) or Mann–Whitney U-tests when data were interval or did not approximate a normal distribution. Bivariate relationships among four categorical ecological variables and parental care (ordinal scale) were also analyzed using Spearman's rank correlation coefficient. Chi-square tests for goodness of fit were used to compare frequency distributions of life-history traits for marine and freshwater fishes.

Nested analysis of covariance was used to test for effects of phylogeny and body size on life-history traits. Order and family were used as independent variables in tests of phylogenetic effects (family nested within order). Mean TL at maturation (ln-transformed) was used as an index of body size. For additional insights into the effects of phylogenetic affiliation on life-history patterns, bivariate relationships among several key life-history variables were analyzed within several orders that contained many species.

To explore patterns of association among life-history traits and ordination of species, a series of principal components analyses (PCA) was performed on ln-transformed life-history data. All PCAs were calculated from the correlation matrix to standardize for the influence of unequal variances. Because data were lacking for some traits for some species, analyses that involved more life-history variables resulted in ordination of fewer species. Therefore, separate PCAs were performed on marine, freshwater, and combined fish data sets: one using 12 relatively nonredundant life-history variables (analyses omitting maximum length (redundant with size at maturity), maximum clutch (redundant with average clutch), range of egg size (redundant with egg size), and either length or age at maturation (highly correlated with each other)) and another using only five life-history variables (length at maturation, mean clutch, egg size, spawning bouts, parental care). The five life-history variables retained for the five-variable analyses were selected based on their dominant influence in the 12-variable PCA models, except that length at maturation was substituted for age at maturity in the five-variable data set in order to increase the number of species retained in the analysis.

Although values for parental care were ordinal, we included ln-transformed parental care values in multivariate analyses because they approximated a normal distribution within most groupings and were derived from an algorithm that combined several independent attributes into a single numeric value. Because some life-history researchers have identified an influence of body size on other life-history traits, some PCAs were done both with and without length partialled-out of the other variables (i.e. multivariate analyses are based on relationships among the residuals from regressions of variables with length). To test for potential biases resulting from disproportionate inclusion of some taxa in the global data set (e.g. *Lepomis* species, $N = 8$), PCA was also performed on a data set containing only one species per genus. The species used to represent genera were selected in alphabetical order to reduce experimenter bias.

To further test relationships between life-history patterns and the species' environmental biology, we performed canonical discriminant function (CDF) based on nine life-history variables and three ecological variables (habitat, trophic status, migration) and parental care recorded as classification variables. CDF derives canonical variables from the set of life-history variables in a manner that maximizes multiple correlations of the original variables within groups. To show general associations between ecological groupings and suites of life-history traits, we plotted the means and standard deviations of each class on the first two CDF axes.

Results

Univariate Comparisons

Life-history parameters showed large variation both within the entire data matrix and within orders containing the largest number of species. Standard deviations approached, and in many instances exceeded, the magnitude of the mean values for life-history traits (Table 1). The pygmy sunfish, *Elassoma zonatum* (Centrarchidae), was the smallest fish in the overall North American data set (minimum size at maturation = 25.0 mm). The largest fishes were the Atlantic sturgeon, *Acipenser oxyrhynchus* (Acipenseridae) (length at maturation = 2.5 m), Pacific halibut, *Hippoglossus stenolepis* (Pleuronectidae) (maximum length = 2.7 m), and ocean sunfish, *Mola mola* (Molidae) (maximum length = 3 m). The smallest maximum clutches (batch fecundities) were recorded for two live bearing surfperches (Embiotocidae), *Hyperprosopon argenteum* (12) and *Cymatogaster aggregata* (20). The largest clutch size estimates were for the ocean sunfish (average = 300×10^6), Atlantic cod, *Gadus morhua* (Gadidae) (maximum = 12×10^6), and tarpon, *Megalops atlanticus* (Elopidae) (maximum = 12.2×10^6). Reported estimates of average egg sizes ranged from a minimum of 0.45 mm in diameter for the bay anchovy, *Anchoa mitchilli* (Engraulidae), to a maximum of 20.5 mm for the mouthbrooding gafftopsail catfish, *Bagre marinus* (Ariidae). Average larval growth rates ranged from a minimum estimate of 1.3 mm TL/mo for lake whitefish, *Coregonus clupeaformis* (Salmonidae), to a high of 69.9 mm TL/mo for longnose gar, *Lepisosteus osseus* (Lepisosteidae).

Comparisons between marine and freshwater fishes showed differences in the distributions of life-history attributes (notable examples illustrated in Fig. 1). Statistically significant mean differences are reported with the following notation: t = value from two-sample *t*-test, z = value from Mann–Whitney U-test. Because both data sets were biased somewhat in favor of larger, commercial species, our interpretations of these univariate comparisons are tentative. As a group, marine fishes matured later (mean marine (m) = 3.38 yr, mean freshwater (f) = 2.74 yr, $t = 1.97$, df = 194, $P < 0.05$; Fig. 1a), matured at larger sizes (m = 320 mm, f = 186 mm, $t = 4.03$, df = 202, $P < 0.0001$), lived longer (m = 13.0 yr, f = 9.7 yr, $t = 2.19$, df = 185, $P < 0.05$), had larger mean clutches (m = 1 554 400, f = 113 376, $t = 4.34$, df = 189, $P < 0.0001$; Fig. 1b), had longer spawning seasons (m = 103 d, f = 59 d, $t = 5.55$, df = 213, $P < 0.0001$; Fig. 1c), had larger YOY growth rates (m = 131.2 mm/yr, f = 98.4 mm/yr, $z = 2.10$, $P < 0.0025$), and had larger adult growth rates (m = 50.8 mm/yr, f = 30.5 mm/yr, $z = 3.12$, $P < 0.001$) than freshwater

TABLE 1. Mean values (standard deviation in parentheses) for 16 life-history variables based on the entire data matrix (all species) and based on seven major fish orders.

Variable	All species	Clupeif.	Salmonif.	Cyprinif.	Silurif.	Percif.	Scorpaenif.	Pleuronectif.
No. of species	216	12	28	30	12	71	16	11
Maximum length (mm TL)	541	323	662	318	414	519	561	894
	(551)	(131)	(438)	(259)	(409)	(551)	(341)	(657)
Age at maturity (yr)	3.0	2.3	3.4	2.7	2.5	2.2	4.7	4.4
	(2.5)	(1.4)	(1.3)	(1.6)	(1.3)	(1.0)	(1.1)	(3.0)
Length at maturity (mm TL)	250	208	339	165	188	199	270	294
	(261)	(104)	(212)	(128)	(139)	(176)	(172)	(74)
Longevity (yr)	11.1	7.7	11.2	7.0	7.6	9.8	24.4	19.7
	(11.4)	(4.3)	(9.5)	(4.2)	(5.1)	(6.5)	(15.1)	(14.2)
Mean clutch size (mature oocytes)	234 000	129 000	13 500	38 000	2 390	356 000	229 000	818 000
	(679 000)	(160 000)	(2 600)	(86 000)	(3 330)	(941 000)	(312 000)	(711 000)
Maximum clutch (mature oocytes)	598 000	258 500	36 500	74 500	8 840	747 500	591 000	2 026 000
	(1 683 000)	(274 000)	(67 500)	(163 500)	(19 826)	(1 746 000)	(709 000)	(1 487 000)
Egg size (mm diameter)	2.14	1.26	3.4	1.81	6.24	1.20	1.37	1.68
	(2.23)	(0.66)	(1.8)	(1.06)	(6.43)	(0.42)	(0.68)	(1.08)
Range egg size (mm diameter)	0.69	0.48	0.93	0.38	2.86	0.29	0.33	1.70
	(1.53)	(0.23)	(0.54)	(0.25)	(4.35)	(0.20)	(0.22)	(3.77)
Spawn season (d)	80	108	50	50	59	91	56	118
	(49)	(49)	(17)	(31)	(25)	(52)	(19)	(63)
Spawn bouts (no./yr)	3.4	18.1	1.1	2.4	1.7	2.7	1.2	1.4
	(14.5)	(51.2)	(0.4)	(3.4)	(0.9)	(5.5)	(0.4)	(1.0)
Parental care (scale 0–8)	1.6	0.2	0.8	1.1	3.4	1.8	3.6	0
	(1.7)	(0.4)	(0.6)	(1.0)	(0.5)	(2.2)	(1.0)	(—)
Hatch time (h)	1111	88	1551	150	253	510	994	165
	(4084)	(68)	(1271)	(88)	(190)	(1522)	(637)	(120)
Larval growth (mm TL/mo)	14.9	19.5	10.8	14.2	13.2	14.0	12.0	13.8
	(10.6)	(16.9)	(8.9)	(8.2)	(3.0)	(7.6)	(—)	(—)
YOY growth (mm TL/yr)	109.9	91.7	133.1	83.6	86.5	115.4	190.8	97.6
	(76.2)	(32.7)	(65.6)	(56.9)	(36.0)	(75.5)	(61.0)	(35.7)
Adult growth (mm TL/yr)	38.5	23.7	58.8	29.4	34.9	36.7	52.9	30.8
	(29.3)	(11.6)	(44.5)	(13.2)	(185)	(24.7)	(19.1)	(10.2)
Fraction growth (% TL/yr)[a]	0.21	0.13	0.23	0.25	0.24	0.21	0.17	(0.22
	(0.12)	(0.08)	(0.12)	(0.16)	(0.16)	(0.09)	(0.07)	(0.08)

[a] Mean percentage of initial TL gained per year of adult life.

fishes. Freshwater fishes tended to have more highly developed parental care than marine fishes ($f = 1.8$, $m = 1.4$, $z = 3.33$, $P < 0.01$; Fig. 1d). Primarily due to skewed distributions, mean maximum clutch sizes ($m = 1\ 102\ 792$, $f = 113{,}376$), mean within-species range of egg diameters ($m = 2.69$, $f = 0.49$), mean hatching times ($m = 786$ h, $f = 1381$ h), and mean larval growth rates ($m = 12.5$ mm/mo, $f = 16.3$ mm/mo) did not differ statistically between groups of fishes classified as marine versus freshwater. Mean fractional adult growth rates were also nearly the same for the two groups ($m = 0.20$, $f = 0.21$). Due to a disproportionate influence of two marine catfishes (Ariidae), mean egg diameters were nearly the same for freshwater and marine fishes ($f = 2.10$ mm, $m = 2.17$ mm), yet distributions of egg size intervals differed significantly (Kolomorov–Smirnov test (K–S), $P < 0.05$; Fig. 1e), and medians differed ($f > m$) based on the nonparametric statistic ($z = 3.78$, $P < 0.0001$). Similarly, after the disproportionate influence of two marine anchovies was reduced through use of the nonparametric test, freshwater fishes tended to have more spawning bouts per year than marine fishes (K–S, $P < 0.05$; $z = 2.15$, $P < 0.05$; Fig. 1f).

Bivariate Life-History Relationships

Correlations between all pairwise combinations of life-history (ln-transformed) and ecological variables are given in Table 2. Some of the high correlations reflect measurement of similar traits or traits that would be expected to covary on a physiological basis (e.g. mean clutch and maximum clutch (0.98), maximum length and length at maturity (0.92), length at maturity and age at maturity (0.77)). Other high correlations need not follow from physiological mechanisms and reflect a diversity of life-history and ecological constraints (e.g. mean clutch and parental care (−0.54), age at maturity and spawning bouts per year (−0.61), longevity and spawning bouts per year (−0.51), length at maturity and YOY growth rate (0.77), mean clutch and YOY growth rate (0.65)).

Figure 2 compares marine and freshwater fishes while illustrating a wide range of bivariate relationships among several of the attributes frequently examined in the life-history literature. The bivariate relationship between ln length at maturity and ln clutch size was nearly the same for fishes categorized as freshwater and marine (Fig. 2a). Neither category showed a strong relationshp between egg size and ln mean clutch size or egg size and ln larval growth rate (Fig. 2b, 2d). The slope was greater for freshwater fishes in the linear relationship between ln mean clutch size and ln YOY growth rate (Fig. 2c), and this difference was due, in part, to the influence of slow YOY growth in cavefishes (*Amblyopsis rosae*, 8.8 mm/yr; *A. spelaea*, 10.6 mm/yr; Poulson 1963).

Correlations between five life-history variables, each measuring an essentially different life-history trait (length at maturity, mean clutch size, egg size, spawning bouts, and parental care), were performed for the seven orders that had the most species with recorded data (Table 3). Overall, matrices of life-history intercorrelations show fairly large deviations among

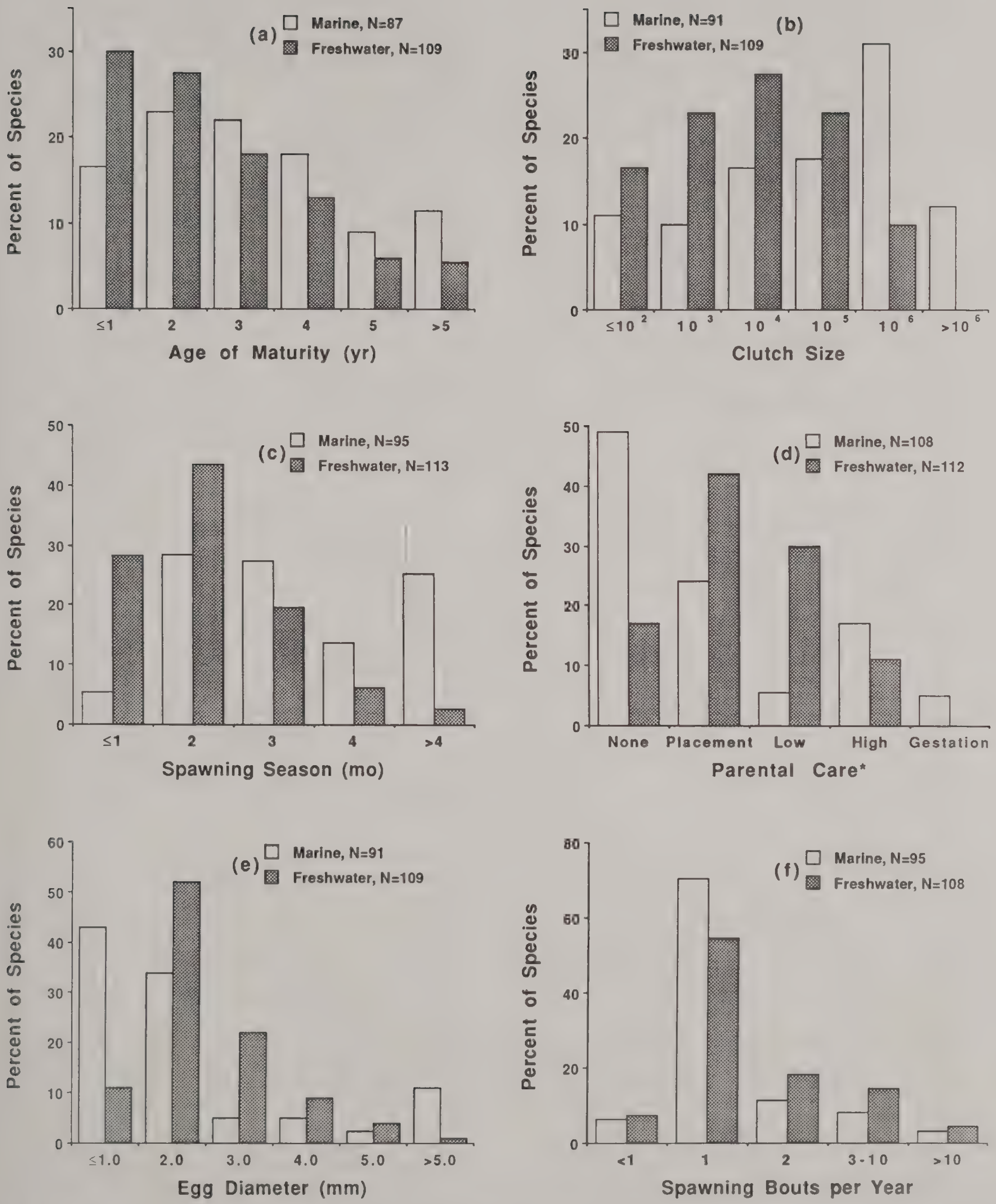

FIG. 1. Frequency distributions of (a) average age at maturation, (b) average clutch size, (c) average duration of the spawning season, (d) parental care (defined under Materials and Methods), (e) average diameter of mature eggs, and (f) average number of spawning bouts per year for fish species classified as either predominantly freshwater or marine.

TABLE 2. Correlation matrix of life-history (ln-transformed) and ecological variables (^{S}Spearman's rank correlation; otherwise, correlations are Pearson's product-moment). Correlations are based on all available data for freshwater and marine species (mean N = 171, range of N = 51–216). *$P < 0.05$; **$P < 0.0001$.

Variable	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. Maximum length	0.71**	0.92**	0.78**	0.75**	0.74**	0.19*	0.17	−0.10	−0.49**	−0.32**	−0.12	0.25*	0.77**	0.76**	−0.32*	−0.10	0.36**	0.14^{S}	0.40^{S}**	0.58^{S}**	0.16^{S}*
2. Age at maturity	—	0.77**	0.80**	0.53**	0.55**	0.37**	0.17	−0.33**	−0.61**	0.03	0.15	0.22*	0.42**	0.39**	−0.38**	0.30**	0.18*	0.01^{S}	0.31^{S}**	0.30^{S}**	0.25^{S}**
3. Length at maturity	—	—	0.75**	0.73**	0.72**	0.24*	0.23*	−0.21*	−0.51**	−0.30**	−0.04	0.26*	0.77**	0.71**	−0.39**	−0.01	−0.36**	0.18^{S}*	0.51^{S}**	0.51^{S}**	0.25^{S}**
4. Longevity	—	—	—	0.66**	0.67**	0.16	0.11	−0.17*	−0.51**	−0.17*	−0.01	0.23*	0.52**	0.44**	−0.43**	0.07	0.16*	0.02^{S}	0.34^{S}**	0.39^{S}**	0.06
5. Mean clutch size	—	—	—	—	0.98**	−0.29*	−0.24*	0.01	−0.37**	−0.54**	−0.45**	0.26*	0.65**	0.58**	−0.34**	- 0.18*	0.40**	0.17^{S}*	0.44^{S}**	0.43^{S}**	0.01
6. Maximum clutch	—	—	—	—	—	−0.30*	−0.26*	0.01	−0.47**	−0.49**	0.39**	0.27*	0.62**	0.55**	−0.36**	−0.19*	0.33**	0.17^{S}*	0.49^{S}**	0.51^{S}**	0.03
7. Egg size	—	—	—	—	—	—	0.76**	−0.35**	−0.19*	0.34**	0.52**	−0.13	0.09	0.19*	−0.01	0.34**	−0.13	−0.06^{S}	−0.21^{S}*	0.02^{S}	0.21^{S}*
8. Range egg size	—	—	—	—	—	—	—	−0.33*	−0.10	0.23*	0.37*	−0.04	0.13	0.13	−0.15	0.26*	−0.21*	0.06^{S}	−0.03^{S}	0.20^{S}*	0.24^{S}*
9. Spawning season	—	—	—	—	—	—	—	—	0.29**	−0.26**	−0.21*	−0.15	−0.14	−0.06	0.13	−0.41**	0.09	0.04^{S}	0.22^{S}**	−0.04^{S}	−0.22^{S}*
10. Spawning bouts	—	—	—	—	—	—	—	—	—	0.00	−0.21*	−0.15	−0.26*	−0.24*	0.22*	−0.08	−0.18	−0.01^{S}	−0.21^{S}*	−0.20^{S}*	−0.20^{S}*
11. Parental care	—	—	—	—	—	—	—	—	—	—	0.37**	−0.07	−0.27*	−0.28*	0.06	0.22*	−0.34**	−0.21^{S}*	−0.29^{S}*	−0.10^{S}	0.01^{S}
12. Hatching time	—	—	—	—	—	—	—	—	—	—	—	−0.26*	−0.27*	−0.06	−0.10	0.49**	−0.19*	−0.04^{S}	−0.08^{S}	−0.02^{S}	0.25^{S}*
13. Larval growth	—	—	—	—	—	—	—	—	—	—	—	—	0.27*	0.17	−0.21*	−0.23*	0.10	0.03^{S}	0.17^{S}	0.06^{S}	−0.06^{S}
14. YOY growth	—	—	—	—	—	—	—	—	—	—	—	—	—	0.69**	−0.42**	−0.11	0.38**	0.20^{S}*	0.39^{S}**	0.39^{S}**	0.14
15. Adult growth	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.16	−0.07	0.28*	0.27^{S}**	0.40^{S}**	0.47^{S}**	0.24^{S}*
16. Fractional growth	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.04	−0.15	0.05^{S}	−0.16^{S}	−0.03^{S}	−0.03^{S}
17. Median latitude	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	−0.35**	−0.27^{S}**	0.04^{S}	0.01^{S}	0.32^{S}**
18. Range latitude	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.31^{S}**	0.46^{S}**	0.25^{S}**	0.05
19. Water column	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.18^{S}*	0.36^{S}**	0.12^{S}
20. Habitat	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.30^{S}**	0.45^{S}**
21. Trophic status	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.04^{S}
22. Migration	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

orders, indicating evolutionary divergences in life-history strategies among higher taxa. Yet, some orders demonstrated high degrees of concordance in the signs of the 10 bivariate relationships, indicating evolutionary conservation or convergences of life-history strategies. Clupeiforms, and siluriforms showed only two of 10 differences in the sign of correlations, and salmoniforms and cypriniforms showed three sign differences, two of which involved $r^2 \leqslant 0.10$. Except for pleuronectiforms (no statistically significant relationship), length at maturity was always positively associated with mean clutch size, and length at maturity was negatively associated with spawning bouts per year. Except for scorpaeniforms (statistically nonsignificant positive relationship), clutch size was always negatively associated with spawning bouts per year (five of six cases were statistically significant; Table 3).

Large positive correlations between life-history and ecological variables (Table 2) were obtained for maximum length with trophic status (0.58), length at maturity with habitat and trophic status (both 0.51), mean clutch size with habitat (0.44), maximum clutch size with habitat (0.49) and trophic status (0.51), hatch time with median latitude (0.49), and adult growth rate with trophic status (0.47). The largest negative correlations between life-history and ecological variables were for length at maturity with range of latitude (−0.36) and parental care with range of latitude (−0.34). The largest positive intercorrelations among ecological variables (Table 2) were for habitat with range of latitude (0.46) and relative migration (0.45). Fishes at higher median latitudes tended to be associated with smaller ranges in latitude (−0.35), and this trend was heavily influenced by marine species.

Multivariate Life-History Patterns

Results of PCA were nearly the same for the data sets involving five life-history variables with all fish species (N = 147) and the data set using only one species to represent each genus (N = 83; Table 4). In each case, the first three PCs modeled 91% of the total variation in the data set and resulted in a first axis with endpoints contrasting species with large body size, large clutches, small eggs, few bouts of reproduction per year, and little parental care against those with small body size, small clutches, multiple reproductive bouts per year, and more parental care. In each case, high scores on the second axis reflect associations of large body size, large eggs, well-developed parental care, and few spawning bouts per year (Table 4). High species scores on the third axis reflect large egg size in association with multiple spawning bouts and little parental care.

When maximum length was partialled-out of the data set containing five life-history variables and 147 species, the first three PC axes modeled 85% of the total variation. The first axis reflected an association of clutches (eigenvector = −0.599), egg size (0.593), and parental care (0.509), and the second axis reflected groupings based on maturation size (0.741) in association with number of bouts of reproduction (−0.626) and clutch size (0.219). The suite of characteristics described by the first orthogonal axis from the length-adjusted analysis was similar to that described by the second axis from the unadjusted analysis. Similarly, the second PC axis from length-adjusted data approximated the primary associations predicted by the first axis from the unadjusted analysis.

With 12 life-history variables, the data set consisting of one species per genus (N = 31) yielded a PCA in which the first three axes modeled 71% of the total variation. The largest variable loadings (eigenvectors) on the first axis were longevity (0.437), age at maturity (0.375), mean clutch (0.375), YOY

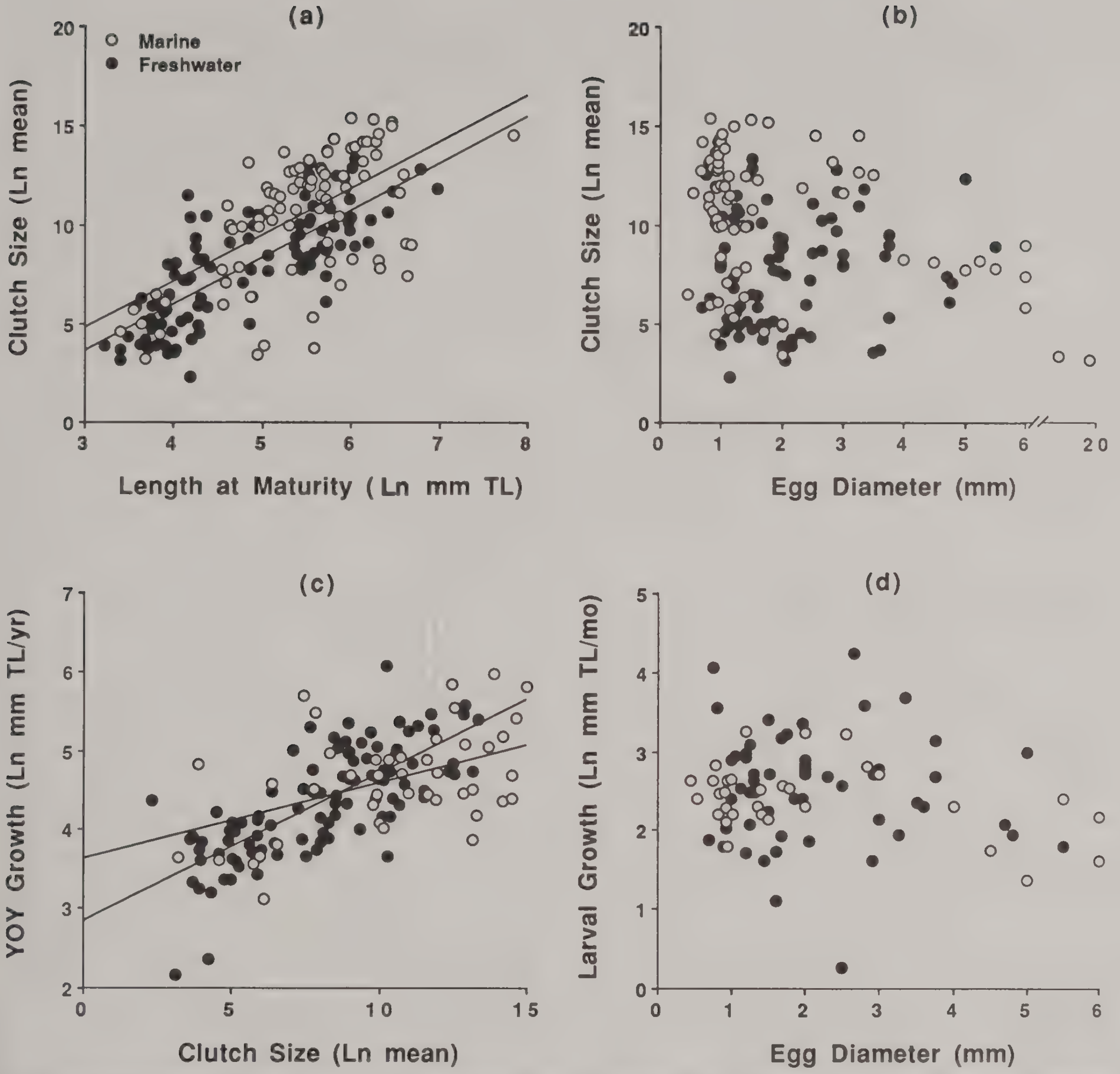

FIG. 2. Bivariate relationships among five life-history traits (open circles = freshwater fishes, closed circles = marine fishes). (a) Freshwater $r^2 = 0.62$, ln clutch = 2.36 (ln length) − 3.48; marine $r^2 = 0.35$, ln clutch = 2.34 (ln length) − 2.24. (b) Freshwater $r^2 < 0.01$; marine $r^2 = 0.17$. (c) Freshwater $r^2 = 0.55$, ln YOY growth = 0.19 (ln clutch) + 2.83; marine $r^2 = 0.35$, ln YOY growth = 0.10 (ln clutch) + 3.63. (d) Freshwater $r^2 < 0.01$; marine $r^2 = 0.20$.

growth (0.348), and spawning bouts (−0.311), and the second axis was dominated by egg size (eigenvector = 0.509), hatch time (0.474), spawning season (−0.407), and parental care (0.397). Based on 12 life-history variables, the PCA using all available fish species ($N = 64$) yielded a PCA that modeled 67% of the total variation. The first axis of this PCA was also dominated by longevity (0.422), age at maturity (0.417), spawning bouts (−0.368), YOY growth (0.346), and mean clutch (0.339), and the second axis was dominated by hatch time (eigenvector = 0.529), egg size (0.509), and mean clutch (−0.340). When maximum length was partialled-out of 12 life-history variables of the all-species data set, the first three PC axes modeled 59% of the total variation. The first axis was dominated by hatch time (eigenvector = 0.439), egg size (0.434), mean clutch (−0.434), and adult growth rate (0.382), and the second axis of the PCA (12 variables with length partialled-out) was dominated by age at maturity (eigenvector = −0.441), longevity (−0.389), spawning bouts (0.359), and YOY growth rate (0.340).

When separate PCAs were performed on data sets that grouped species as either freshwater or marine (unadjusted for length), the variable loadings on the first three PC axes predicted suites of life-history characteristics very similar to those revealed by the combined species data sets. Each of four analyses (freshwater versus marine, 12 versus five life-history variables; based on unadjusted values) identified a continuum of

TABLE 3. Pearson product-moment correlations among five life-history variables by fish order. All variables were ln-transformed. $*P < 0.05$; $**P < 0.0001$; ×, no variation recorded in one variable.

Variable	Clutch size	Egg size	Spawn bouts	Parental care
Clupeiformes (N = 12)				
Length at maturity	0.87*	0.74*	−0.81*	0.54
Mean clutch size	—	0.41	−0.83*	0.50
Egg size	—	—	−0.45	0.26
Spawn bouts	—	—	—	−0.38
Cypriniformes (N = 27)				
Length at maturity	0.78**	0.71*	−0.54*	−0.35
Mean clutch size	—	0.55*	−0.65*	−0.54*
Egg size	—	—	−0.38	−0.10
Spawn bouts	—	—	—	0.36
Perciformes (N = 58)				
Length at maturity	0.88**	−0.18	−0.67**	−0.45*
Mean clutch size	—	−0.48*	−0.54**	−0.65**
Egg size	—	—	0.38*	0.59**
Spawn bouts	—	—	—	0.19
Pleuronectiformes (N = 11)				
Length at maturity	−0.08	−0.34	0.14	×
Mean clutch size	—	−0.27	−0.68*	×
Egg size	—	—	−0.24	×
Salmoniformes (N = 28)				
Length at maturity	0.28	0.71**	−0.31	−0.18
Mean clutch size	—	−0.24	−0.16	−0.44*
Egg size	—	—	−0.43*	0.07
Spawn bouts	—	—	—	−0.04
Siluriformes (N = 12)				
Length at maturity	0.78*	0.26	−0.67*	0.47
Mean clutch size	—	−0.46	−0.72*	0.19
Egg size	—	—	0.41	0.43
Spawn bouts	—	—	—	−0.28
Scorpaeniformes (n = 14)				
Length at maturity	0.57*	0.06	−0.29	0.11
Mean clutch size	—	−0.44	0.40	−0.19
Egg size	—	—	−0.01	0.05
Spawn bouts	—	—	—	−0.40

life-history strategies with large size at maturity (or late maturity), large clutches, few spawning bouts per year, and little parental care on one end and small size at maturity (or early maturity), small clutches, multiple spawning bouts, and more parental care on the other (Table 5). This continuum was associated with the first PC for the freshwater group (based on both 12 and five variables) and the marine group based on five variables, but was associated with the second PC for the marine group based on 12 life-history variables (Table 5). The separate freshwater and marine analyses each identified a second basic life-history continuum that revealed an association between smaller clutches, larger eggs, and more parental care. This axis was identified by the second PC in the freshwater group (both 12 and five variables) and the first PC (12 variables) and second PC (five variables) in the marine group (Table 5).

The ordination of species based on the first two axes of PCA (based on five life-history variables; unadjusted for length) shows a large range of life-history strategies for most orders within both the freshwater (Fig. 3) and marine (Fig. 4) groups. Relative to other freshwater fishes, lake sturgeon (*Acipenser fulvescens*) and paddlefish (*Polyodon spathula*) exhibit an extreme strategy (i.e. extreme positive values on abscissa in Fig. 3) in which age and size at maturation are large, eggs are numerous and small in relation to body size, and spawning is episodic and seasonal. Salmon and trout (*Oncorhynchus, Salmo, Salvelinus* spp.) display a variation of this strategy that involves smaller clutches and greater egg size in relation to body size. Cavefishes (Amblyopsidae) and madtom catfishes (*Noturus* spp.) exhibit a different strategy (upper left region in Fig. 3) that involves large egg size relative to body size and parental care (branchial brooding in cavefishes, nest guarding in certain madtoms). Certain species of darters (*Etheostoma, Percina* spp.) and minnows (Cyprinidae) exhibit a strategy of early maturation and multiple spawning of small clutches consisting of small eggs. A life-history strategy consisting of large maturation size and episodic or seasonal spawning of large clutches of small eggs (lower right region in Fig. 3) is displayed by a taxonomically diverse group of fishes, including the gizzard shad (*Dorosoma cepedianum*), muskellunge (*Esox masquinongy*), burbot (*Lota lota*), and suckers (*Catostomus, Moxostoma* spp.)

The pattern of ordination of marine fishes on the first two PCs (Fig. 4) followed a pattern very similar to that shown by freshwater fishes. Sturgeons again represented an extreme example of the delayed-maturation, large-clutch, periodic-spawning strategy that involves large eggs in absolute sense, but small eggs relative to body size (points on the right-hand half of Fig. 4). Again, salmon exhibited a strategy of low-frequency spawning but larger relative egg sizes and much smaller clutches. The large-clutch, episodic-spawning strategy involving small eggs can be seen in a phylogenetically diverse mixture of fishes, including the Atlantic cod, striped bass (*Morone saxatilis*), cobia (*Rachycentron canadum*), skipjack tuna (*Katsuwonus pelamis*), red snapper (*Lutjanus campechanus*), and winter founder (*Pleuronectes americanus*). Relatively few of the marine fishes fell within the region of large egg size and parental care (upper left region in Fig. 4), but an extreme form of this life-history strategy is seen in the mouthbrooding sea catfishes (*Arius felis, B. marinus*). The strategy of rapid maturation at small sizes and production of multiple small clutches of small eggs (lower left region in Fig. 4) is seen in the bay anchovy, mummichog (*Fundulus heteroclitus*), and inland silverside. Small fishes with parental care lie intermediate between the parental care strategy and early-maturation, multiple-clutch strategy and include the threespine stickleback, gulf pipefish (*Syngnathus scovelli*), and the blackbelly eelpout (*Lycodopsis pacifica*).

Phylogenetic and Ecological Correlates of Life-History Strategies

Mean values for most life-history parameters (length, longevity, clutch size, egg size, parental care, hatch time) varied considerably among fish orders (Table 1). Relative to other life-history variables, larval growth rates (12.0–19.5 mm/mo) and average fractional adult growth rate (proportion of adult TL gained per year = 0.13–0.25) showed the least variability among orders. Phylogenetic affiliations are also apparent in the general pattern of ordination of species within orders in the plots of species scores on the first two PC axes (Fig. 3, 4). Based on ANCOVA, statistically significant effects of phylogeny at the ordinal and family levels were obtained for 15 ln-

TABLE 4. PCA statistics for the North American fish data matrix based on five life-history variables and using all species ($N = 147$ species) and one representative per genus ($N = 83$ genera). Variable loadings (eigenvectors) on the first three principal axes that were between −0.250 and 0 are listed as −, and those between 0 and 0.250 are listed as +.

	All species			One species per genus		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	2.346	1.496	0.688	2.417	1.459	0.696
% variance	46.9	29.9	13.8	48.3	29.2	13.9
Variable						
Length at maturity	0.558	0.290	+	0.498	0.384	0.347
Mean clutch size	0.602	−	−	0.613	−	−
Egg size	—	0.706	0.561	−0.253	0.625	0.582
Spawning bouts	−0.372	−0.465	0.604	−	−0.601	0.652
Parental care	−0.425	0.419	−0.494	−0.507	0.318	−0.334

TABLE 5. PCA statistics for North American freshwater fish data matrices based on 12 and five ln-transformed life-history variables. Data on the left-hand side are for freshwater fishes, and data on the right-hand side are for marine fishes. Variable loadings (eigenvectors) on the first three principal axes that were between −0.250 and 0 are listed as −, and those between 0 and 0.250 are listed as +.

	PC1	PC2	PC3	PC1	PC2	PC3
	Freshwater species $N = 44$			*Marine species* $N = 20$		
Eigenvalue	4.898	2.059	1.061	3.979	3.450	1.873
% variance	40.8	17.2	8.8	33.2	28.7	15.6
Variable						
Age at maturity	0.372	+	+	−	0.504	−
Longevity	0.400	−	+	−	0.464	−
Mean clutch size	0.306	−0.397	−	−0.270	0.357	+
Egg size	+	0.531	+	0.426	+	−
Spawning season	−	−	+	−0.346	−0.274	+
Spawning bouts	−0.320	−	−	−	−0.431	−
Parental care	−	−	0.854	0.288	+	−0.402
Hatching time	+	0.580	−0.255	0.463	−	−
Larval growth	+	−0.389	−	−0.305	+	+
YOY growth	0.368	−	+	+	+	0.648
Adult growth	0.347	−	−	0.319	+	0.497
Fractional growth	−0.268	+	−	0.316	−	0.264
	Freshwater species $N = 82$			*Marine species* $N = 65$		
Eigenvalue	2.457	1.142	0.823	2.157	1.810	0.584
% variance	49.1	22.9	16.4	43.1	36.2	11.7
Variable						
Length at maturity	0.596	+	+	0.450	0.466	0.371
Mean clutch size	0.526	−0.361	−0.281	0.641	−	−
Egg size	0.267	0.696	0.551	−0.256	0.601	0.517
Spawning bouts	−0.421	−0.363	−0.511	−0.400	−0.460	0.516
Parental care	−0.345	0.502	−0.597	−0.401	0.449	−0.566

transformed life-history variables (Table 6). Except for the lack of a significant family effect on adult growth rate, significant effects for the nested ANCOVA type III sum of squares show that phylogenetic effects are present even after the influence of length (maximum TL) as a covariate and the effects of ordinal affiliations for families were removed (Table 6). Relationships between maximum length and three variables (range of egg size, hatching time, duration of spawning season) were not statistically significant within the total fish data set (Tables 2, 6).

Each of the four discriminant function analyses (CDF) resulted in a first canonical axis in which high values corresponded with larger size at maturity, larger clutches, longer life span, and faster growth (Fig. 5; Table 7). When migration was used as the class variable, the first axis was also associated with larger egg size. The second canonical axis was more discordant between tests involving different class variables (Table 7).

The CDF using habitat as the class variable (Fig. 5a) showed a general pattern of larger, longer-lived fishes with large clutches and short spawning seasons in association with the marine environment, estuaries, river backwaters, and lakes versus small fishes with small clutches, slow YOY growth, and long spawning seasons in association with headwater habitats. River fishes were intermediate between headwater and estuarine/marine fishes in the multivariate life-history space defined

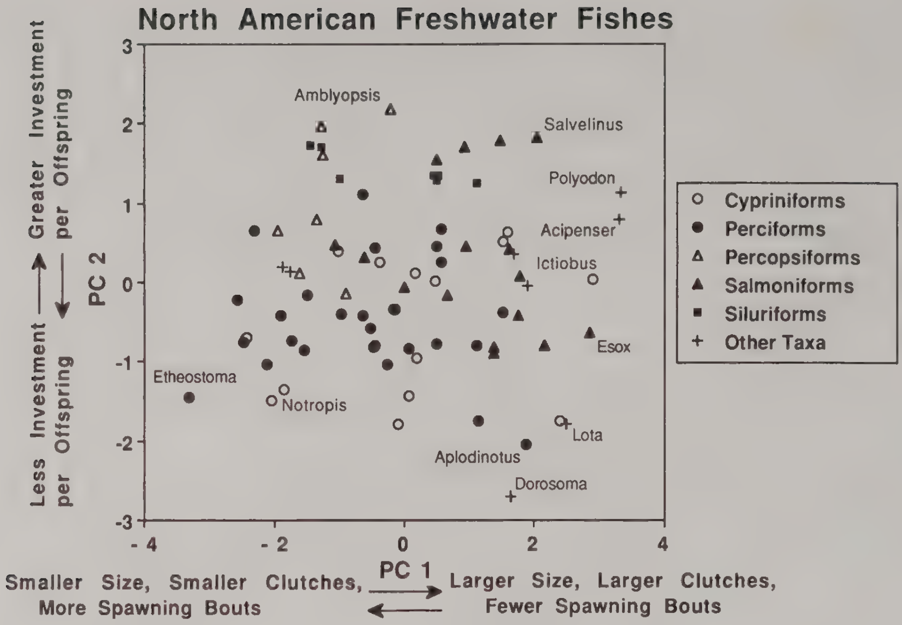

FIG. 3. Scores for freshwater fish species on the first two principle components axes based on five life-history variables (length at maturity, average clutch, egg size, bouts per year, parental care). The two axes are interpreted based on correlations of the original life-history variables (statistics associated with the PCA are given in Table 5).

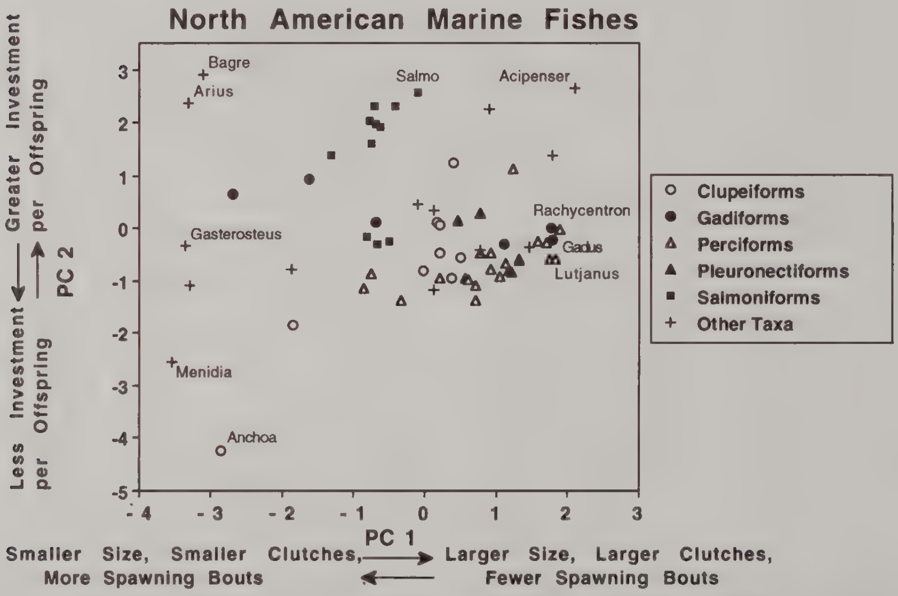

FIG. 4. Scores for marine fish species on the first two principle components axes based on five life-history variables (length at maturity, average clutch, egg size, bouts per year, parental care). The two axes are interpreted based on correlations of the original life-history variables (statistics associated with the PCA are given in Table 6).

by CDF. The CDF based on trophic status (Fig. 5b) showed a general pattern of larger, longer-lived fishes with large clutches, intermediate-sized eggs, and little parental care in association with piscivory versus small fishes with small clutches, slow YOY growth, larger eggs, and more parental care in association with feeding on invertebrates and omnivory. In addition, detritivores tended to be associated with small size, small clutches, small eggs, and little or no parental care (Fig. 5b).

Highly migratory fishes (Fig. 5c) were associated with large body size, long life spans, and large clutches. Catadromous fishes (represented by the American eel, *Anguilla rostrata*) exhibited a lower spawning frequency (i.e. one semelparous

TABLE 6. Results of nested ANCOVA for life-history variables (ln-transformed) with family nested within order and maximum total length as a covariate. Type I sum of squares (SS) are for main effects of variables without adjustment for size effects; Type III SS are for effects of family and order after adjustment for covariation due to size.

Variable		Type I SS		Type III SS		Model r^2
		F	P	F	P	
Age at maturity	Order	16.7	0.0001	5.8	0.0001	0.80
	Family (order)	4.0	0.0001	2.7	0.0001	
	Max. length	110.0	0.0001			
Length at maturity	Order	32.7	0.0001	1.5	0.082	0.91
	Family (order)	16.2	0.0001	1.7	0.015	
	Max. length	317.4	0.0001			
Longevity	Order	14.3	0.0001	2.4	0.0013	0.81
	Family (order)	6.0	0.0001	2.3	0.0012	
	Max. length	91.9	0.0001			
Mean clutch size	Order	27.8	0.0001	7.8	0.0001	0.91
	Family (order)	19.6	0.0001	9.8	0.0001	
	Max. length	149.3	0.0001			
Maximum clutch	Order	26.5	0.0001	8.7	0.0001	0.92
	Family (order)	22.9	0.0001	10.7	0.0001	
	Max. length	171.3	0.0001			
Egg size	Order	14.9	0.0001	11.2	0.0001	0.80
	Family (order)	5.3	0.0001	5.1	0.0001	
	Max. length	8.5	0.0042			
Range egg size	Order	4.7	0.0001	5.4	0.0001	0.70
	Family (order)	4.1	0.0001	4.0	0.0001	
	Max. length	3.8	0.055			
Spawning season	Order	5.5	0.0001	6.2	0.0001	0.57
	Family (order)	2.5	0.0003	2.7	0.0001	
	Max. length	1.9	0.16			
Spawning bouts	Order	8.8	0.0001	5.9	0.0001	0.70
	Family (order)	4.4	0.0001	2.8	0.0001	
	Max. length	36.2	0.0001			
Parental care	Order	12.2	0.001	9.5	0.0001	0.79
	Family (order)	8.7	0.0001	7.5	0.0001	
	Max. length	16.2	0.0001			
Hatching time	Order	14.6	0.0001	5.0	0.0001	0.83
	Family (order)	9.5	0.0001	9.1	0.0001	
	Max. length	1.2	0.26			
Larval growth	Order	2.0	0.028	1.4	0.15	0.47
	Family (order)	1.5	0.14	1.1	0.34	
	Max. length	4.3	0.042			
YOY growth	Order	10.4	0.0001	2.7	0.0006	0.79
	Family (order)	7.2	0.0001	1.8	0.026	
	Max. length	36.7	0.0001			
Adult growth	Order	8.8	0.0001	2.7	0.0009	0.75
	Family (order)	5.6	0.0001	1.3	0.18	
	Max. length	75.3	0.0001			
Fractional adult growth	Order	2.9	0.0005	2.1	0.013	0.46
	Family (order)	2.1	0.011	1.6	0.058	
	Max. length	6.3	0.013			

bout per 14 yr of adult life on average) and smaller egg size when compared with anadromous fishes (primarily salmon) with earlier maturation. Less-migratory fishes tended to be smaller with relatively smaller clutches and smaller eggs than migratory species; however, highly sedentary fishes tended to have longer spawning seasons and larger eggs than migratory fishes.

When CDF was performed with level of parental care as the class variable (none, placement of eggs into a special habitat, low guarding, high guarding/viviparity), fishes with highly developed parental care were associated with the small size, short life spans, small clutches, slow YOY and adult growth, and spawning seasons of intermediate length (Fig. 5d). Fishes with no parental care tended to be large with long lifespans,

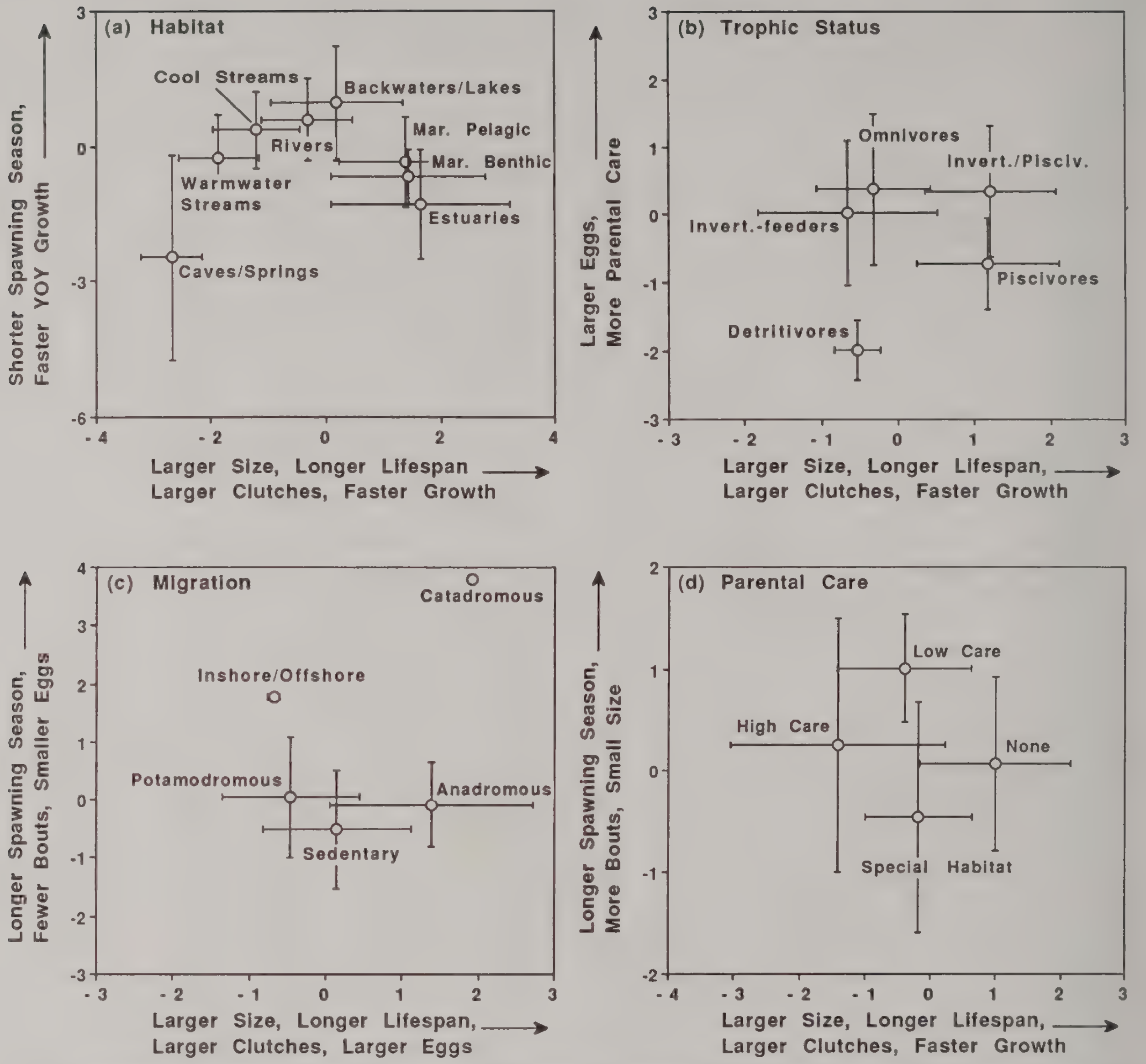

FIG. 5. Average species scores on the first two discriminant function axes by ecological and life-history groupings. Discriminant functions for a–c were based on nine life-history variables (length at maturity, average clutch, egg size, longevity, spawning season, bouts per year, YOY growth, adult growth, parental care), and plot d was based on eight variables with parental care as the grouping variable. The x-axis represents the first canonical axis, the y-axis is the second canonical axis, and verbal interpretations of axes are based on the eigenvectors of the original life-history variables. Statistics associated with each plot are summarized in Table 7.

large clutches, fast YOY and adult growth, and intermediate breeding seasons. Fishes exhibiting no parental care other than special placement of eggs (e.g. scattering over vegetation or gravel beds) tended to be smaller and less fecund with shorter spawning seasons than the group with no parental care. Fishes with low levels of parental care (e.g. brief period of nest guarding by the male) tended toward small body size, intermediate clutches, intermediate YOY growth rates, and longer spawning seasons involving multiple bouts.

Discussion

Life history trade-offs frequently are sought by means of bivariate regression analysis of attributes having a hypothesized functional relationship. For example, one way to achieve larger clutches is to partition reproductive biomass into smaller individual packages, which yields the negative correlation between clutch size and egg size frequently observed in fishes (Wootton 1984; Duarte and Alcarez 1989; Elgar 1990; Fleming and Gross 1990; Paine 1990). In the current study, egg size showed a significant, but weak, inverse relationship with clutch size when the comparison was based on the entire data set ($r = -0.29$, $P < 0.05$). This pattern is not due to a clutch size – body size interaction because many fishes (e.g. *B. marinus*) have much smaller clutches than species of much smaller body size (e.g. *Rhinichthys atratulus* (blacknose dace)). A negative relationship between clutch size and egg size was obtained for

TABLE 7. Statistics associated with canonical discriminant function analyses based on three ecological and one life-history classification variables: habitat, trophic status, migration, and parental care. *P* values for discriminant function axes represent the probability that canonical correlation for the axis and all that follow are zero (probability that Wilks' lambda $> F$); coefficients for variables are based on total canonical structure.

	Habitat		Trophic status		Migration		Parental care	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	2.054	1.142	0.869	0.221	0.555	0.219	0.563	0.289
Variance	0.42	0.23	0.67	0.17	0.60	0.24	0.60	0.31
P	0.0001	0.0001	0.0001	0.14	0.0001	0.09	0.0001	0.0023
Variable								
Length maturity	0.727	0.252	0.702	–	0.757	–	0.513	−0.743
Longevity	0.508	0.328	0.387	–	0.395	–	0.391	−0.537
Mean clutch	0.891	+	0.595	−0.347	0.447	0.265	0.770	−0.352
Egg size	–	0.285	0.232	0.655	0.419	−0.466	−0.386	−0.351
Spawn season	0.324	−0.677	–	–	−0.271	0.684	0.435	0.548
Spawn bouts	–	+	−0.260	–	−0.505	−0.464	+	0.477
Parental care	−0.692	–	+	0.525	+	+		
YOY growth	0.658	0.552	0.753	−0.335	0.326	–	0.623	−0.308
Adult growth	0.663	+	0.890	–	0.628	–	0.428	−0.551

perciforms, pleuronectiforms, salmoniforms, siluriforms, and scorpaeniforms, but the relationship was actually positive for clupeiforms and cypriniforms. Our data set, which involved a broader taxonomic and ecological survey than that used by Duarte and Alcarez (1989), indicates that larger clutches may indeed be produced by either delaying reproduction until achieving a large body size or packaging reproductive biomass into smaller eggs or both. However, not all of the narrower ecological or taxonomic groupings of fishes were consistent with these simple functional trade-offs. Simultaneous trade-offs with other life-history attributes can account for low correlations in instances in which strong functional relationships are hypothesized. Greater insights into the potential adaptive significance of individual attributes often can be gained by examining their interrelationships by multivariate methods. Much of the variance around a bivariate regression often can be explained by simultaneous trade-offs by one or both of the two life-history attributes with other attributes.

Life-History Patterns as Adaptive Strategies

Multivariate methods identified two general gradients of variation that were fairly consistent among the various subsets of life-history variables and species. In one form or another, a principal association was found between larger adult body size with delayed maturation, longer life span, larger clutches, smaller eggs, and fewer annual spawning bouts. In most data sets, a second orthogonal gradient contrasted fishes having more parental care, larger eggs, longer spawning seasons, and multiple bouts against fishes with the opposite suite of traits. When body length was partialled-out of the other life history traits, most of the strong associations were retained. When species are ordered simultaneously on the two primary gradients, three fairly distinctive life-history strategies are identified as the endpoints of a trilateral continuum (Fig. 3, 4). In most instances, the addition of a life-history gradient derived from a third or fourth axis produced little modification in the general pattern of species ordination derived from the first two principal axes.

The three primary strategies (i.e. endpoint strategies) of North American fishes have some striking similarities with earlier patterns presented in the empirical and theoretical life-history literature. We observed (1) species with delayed maturation, intermediate or large size at maturation, large clutches, small eggs, rapid larval and YOY growth rates, and short reproductive seasons, (2) species with early maturation, small size at maturation, small eggs, rapid larval growth, and long reproductive seasons with multiple spawning bouts, and (3) small- or medium-size species with large eggs, small clutches, well-developed parental care, slow YOY and adult growth, and long reproductive seasons. Freshwater fishes have a more restricted range of strategies within life-history space than marine fishes when the two groups are viewed jointly. When we plotted the first two PC coordinates of freshwater and marine fishes together (species loadings associated with Table 4), the orientation and shape of the scatterplot were very similar to Fig. 4, and each of the three endpoints was a marine representative (i.e. bay anchovy, gafftopsail catfish, Atlantic sturgeon).

We observe great consistency among the gradients of life-history variation here and among those derived from comparisons of commerical stocks of marine fishes (Kawasaki 1980, 1983), Pacific surfperches (Baltz 1984), neotropical freshwater fishes (Winemiller 1989), and North American darters (Paine 1990). Wootton (1984) clustered on Canadian freshwater fishes based on five variables reported in Scott and Crossman (1973). He discussed three prinicpal life-history groupings: (1) salmonid fishes with fall/winter spawning, large eggs, large body size, and low relative fecundity, (2) small species with low fecundities, short life spans, and spring/summer spawning, and (3) medium and large species with high fecundities, small eggs, and spring spawning. Based on fishes from a Canadian and a Polish river system, Mahon (1984) interpreted the pattern of species ordination on the first axes of PCA as a gradient of reproductive strategies correlated with a gradient of fluvial habitats (i.e. small, early-maturing, sedentary fishes with parental care and few large eggs in headwaters versus larger migratory fishes with the opposite suite of characteristics in large rivers). Mahon interpreted the second PC gradient as a trade-off between egg size and fecundity.

Given that populations exhibiting these divergent strategies are persistent, insights into population regulation can be gained by comparing suites of life-history traits in the context of adaptations for alternative environmental conditions (Southwood 1988). Next we discuss some hypothesized relationships between primary strategies, life-history trade-offs, and selection caused by different scales of environmental variation.

Periodic strategy

Following Winemiller's (1992) terminology, a "periodic" strategy identifies fishes that delay maturation in order to attain a size sufficient for production of a large clutch and adult survival during periods of suboptimal environmental conditions (e.g. winter, dry season, periods of reduced food availability). Species with large clutches frequently reproduce in synchronous episodes of spawning, and this trend yielded the negative association between clutch size and number of spawning bouts per year. This synchronous spawning often coincides either with movement into favorable habitats or with favorable periods within the temporal cycle of the environment (e.g. spring). Extreme forms of the high-fecundity strategy are often seen among marine species with pelagic eggs and larvae (e.g. cod, cobia, tuna, ocean sunfish). These marine species appear to cope with large-scale spatial heterogeneity of the marine pelagic environment by producing huge numbers of tiny offspring, at least some of which are bound to thrive once they encounter favorable areas or patches within zones and strata. Yet, on average, larval survivorship is extremely low among highly fecund fishes in the marine environment (Houde 1987). Miller et al. (1988) argued that the average larval fish dies during the first week of life, and greater understanding of recruitment may be achieved by seeking greater understanding of the unique features of survivors. Within a local population, some spawners probably contribute disproportionately large numbers of survivors to subsequent generations (relative to conspecifics with similar clutch sizes) based on purely stochastic aspects of larval movement into favorable zones. Despite the fact that egg size tends to be small in periodic fishes, both larval and YOY growth rates tended to be relatively fast. We presume that these fast growth rates for early life stages reflect assimilation from exogeneous feeding by the early survivors that encounter relatively high prey densities. This is consistent with Houde's (1989) assumption that higher growth rates for marine fish larvae at higher temperatures are supported by increased food consumption rather than increased growth efficiency.

At temperate latitudes, large-scale temporal variation in environmental conditions may be as influential as spatial variation on the timing of reproduction. Temporal variation at high latitudes is large and cyclic, hence to some extent predictable. In theory, highly fecund fishes can exploit predictable patterns in time or space by releasing massive numbers of small progeny in phase with periods in which environmental conditions are most favorable for larval growth and survival (Cohen 1967; Boyce 1979). Natural selection should strongly favor physiological mechanisms that enhance a fish's ability to detect cues that predict the moment of a periodic cycle (e.g. photoperiod, ambient temperature, solute concentrations). In the marine pelagic environemnt at low latitudes, large-scale variation in space may represent a periodic signal as strong as seasonal variation at temperate latitudes (i.e. patchily distributed physical parameters, primary production, zooplankton, etc., due to upwellings, gyres, convergence zones, and other predictable currents; Sinclair 1988; MacCall 1990).

Periodic strategists are among the most migratory of North American fishes, an association also revealed by Roff's (1988) analysis of marine fishes and observed among South American freshwater fishes (Winemiller 1989). In California, anadromous threespine stickleback were more periodic in their characteristics (e.g. large clutches, larger size at maturity) when compared with freshwater populations (Snyder 1990). Migration to favorable habitats for spawning is a means by which fishes can reduce uncertainty in their attempts to exploit large-scale temporal and spatial environmental variation. For example, American shad (*Alosa sapidissima*) are more iteroparous and devote a greater fraction of energy to migration at middle and higher latitudes where environments are less stable and less predictable (Leggett and Carscadden 1978). Rothschild and DiNardo (1987) viewed anadromy as a means by which adults seek favorable environments for larval development whereas the reproductive success of marine broadcast spawners may depend on rates of encounters by larvae with suitable zones or patches. Massive clutches of small eggs undoubtedly enhance dispersal capabilities of wide-ranging marine fishes during the early life stages. In a stable population, losses due to advection ultimately are balanced by the survival benefits derived from the passage of some fraction of larval cohorts into suitable regions or habitats (Sinclair 1988).

Opportunistic strategy

The "opportunistic" life-history strategy in fishes appears to place a premium on early maturation, frequent reproduction over an extended spawning season, rapid larval growth, and rapid population turnover rates, all leading to a large intrinsic rate of population increase (Winemiller 1989, 1992). Opportunistic fishes differ markedly from the *r*-strategists of Pianka (1970) and others in having among the smallest rather than largest clutches. The strong inverse relationship between the rate of population growth and generation time has been appreciated for a long time (Birch 1948; Smith 1954; Lewontin 1965; Pianka 1970; Michod 1979). Small fishes with early maturation, small eggs, small clutches (yet high relative reproductive effort), and continuous spawning are well equipped to repopulate habitats following disturbances or in the face of continuous high mortality in the adult stage (Lewontin 1965). This suite of life-history traits permits efficient recolonization of habitats over relatively small spatial scales. Extreme examples of the opportunistic strategy are seen in the bay anchovy, silversides, killifishes (*Fundulus* spp.), and mosquitofishes (*Gambusia* spp). These small fishes frequently maintain dense populations in marginal habitats (e.g. ecotones, constantly changing habitats) and frequently experience high predation mortality during the adult stage.

Equilibrium strategy

The "equilibrium" strategy in fishes is largely consistent with the suite of characteristics often associated with the traditional *K*-strategy of adaptation to life in resource-limited or density-dependent environments (Pianka 1970). Large eggs and parental care result in the production of relatively small clutches of larger or more advanced juveniles at the onset of independent life. Our equilibrium strategy differs from the traditional *K*-strategy model in that equilibrium strategists tended to rank among the smallest fishes rather than largest (the largest North American fishes were periodic strategists). Within the North American fish data set, marine ariid catfishes (egg diameters 16.0–20.5 mm, oral brooding of eggs and larvae) and amblyopsid cavefishes (branchial brooding of small clutches of relatively large eggs) represent extreme forms of the equilibrium life-history strategy. Cavefishes probably inhabit the most temporally stable and resource limited of the aquatic environments covered in our survey.

Intermediate strategies

Three endpoint life-history strategies are fairly distinctive, but intermediate strategies are also recognized near the center and along the boundaries of a trilateral gradient. Some of the largest periodic strategists (e.g. lake sturgeon, paddlefish) have relatively large eggs, which compromises the attainment of a theoretical maximum clutch size. Salmon and trout possess much larger eggs and smaller clutches than fishes exhibiting the extreme periodic life-history configuration. An inverse relationship between egg size and clutch size was found within the salmoniforms (Table 3). Among populations of coho salmon (*Oncorhynchus kisutch*), this inverse relationship is observed over a latitudinal gradient of declining egg size and increasing clutch size with increasing latitude (Fleming and Gross 1990). Fleming and Gross suggested that selection favors local optima in egg size with clutch size adjustments resulting from physiological constraints and ecological performance. Relative to periodic strategists with larger clutches and smaller eggs, salmon and trout appear to have adopted a more equilibrium strategy of larger investment in fewer offspring and larger offspring at the time of independent life. Migration to special spawning habitats and burial of zygotes (brood hiding) by salmon, char, and trout could be viewed as forms of parental investment that carry large energetic and survival costs in relation to future reproductive effort.

A number of medium-size fishes have seasonal spawning, moderately large clutches, and male nest guarding (e.g. *Ameiurus* spp., *Lepomis* spp.). Another intermediate group has large clutches, small eggs, and viviparity (e.g. *Sebastes* spp.). These fishes are in between the periodic and equilibrium endpoints of the gradient. Small fishes with rapid maturation, small clutches, large eggs relative to body size, and a degree of parental care (e.g. *Pimephales* spp., *Noturus* spp., *Etheostoma* spp., *G. aculeatus, S. scovelli, Cottus* spp.) lie between the opportunistic and equilibrium strategists. Similarly, small fishes with seasonal spawning, moderately large clutches, small eggs, and only one or a few bouts of reproduction per season (e.g. *Osmerus mordax* (rainbow smelt), *Notemigonus crysoleucas* (golden shiner), *Notropis* spp., *Percopsis omiscomaycus* (trout-perch) lie between the opportunistic and periodic strategists on the gradient. Determinations of multiple spawning in fishes have been difficult (Heins and Rabito 1986; Heins and Baker 1988), and we suspect that some of the small North American fishes categorized as single spawners (and some species conservatively coded as two bouts per year here) may actually spawn several times each season. With improved estimates of multiple spawning, some of the small fishes intermediate between opportunistic and periodic strategists may actually cluster nearer the opportunistic endpoint.

Life-History Strategies and Population Regulation

Life-history theory attempts to explain patterns of covariation in demographic parameters and reproductive traits in relation to alternative environmental conditions (Lack 1954; Stearns 1976; Whittaker and Goodman 1979; Southwood 1988). For example, Murphy (1968) and Kawasaki (1980, 1983) each concluded that delayed maturation, iteroparity, and high fecundity increase the probability of recruitment to the adult population in the face of variable preadult mortality in marine environments. Armstrong and Shelton (1990) used a Monte Carlo model to show that within-season serial spawning reduces variation in clupeoid brood strength when within-season variation is large. Several other studies have explored the potential influence of alternative life-history strategies on fish population responses to both natural and anthropogenic disturbances (Adams 1980; Saunders and Finn 1983; Garrod and Horwood 1984; Ware 1984; Rago and Goodyear 1987; Schaaf et al. 1987; Barnthouse et al. 1990; Beverton 1990; Leaman 1991).

Following Winemiller (1992), we propose that the essential features of the three primary life-history strategies can be captured by the interrelationships among three basic demographic parameters: survival, fecundity, and onset and duration of reproductive life. In terms of life-history strategies, fitness can be estimated by either V_x, the reproductive value of an individual or age class (Fischer 1958; Pianka 1976; Leaman 1991), or r, the intrinsic rate of natural increase of a population or genotype (Birch 1948; Cole 1954; Southwood et al. 1974; Roff 1984; Stearns and Crandall 1984), or λ, the finite rate of growth from the Euler equation (and see Ware (1982, 1984) for discussions of surplus power as a measure of fitness). Each of these fitness measures can be expressed as a function of three essential components: survivorship, fecundity, and the onset and duration of reproductive life. In the case of reproductive value:

$$(2) \quad V_x = m_x + \sum_{t=x+1}^{\omega} \frac{l_t\, m_t}{l_x}$$

where for a stable population, m_x is age-specific fecundity, l_x is age-specific survivorship, and ω is the last age class of active reproduction. In this form of the equation, two components of reproductive value are added together: the current investment in offspring (m_x) and the expectation of future offspring (residual reproductive value). Reproductive value is therefore equivalent to the lifetime expectation of offspring (i.e. provided that x is equal to α, the age at first reproduction) and contains survivorship, fecundity, and timing components.

The intrinsic rate of population increase can be approximated as

$$(3) \quad r \simeq \frac{\ln R_0}{T}$$

where R_0 is the net replacement rate, T is the mean generation time ($T \simeq \sum_{x=\alpha}^{\omega} x\, l_x\, m_x$), and

$$(4) \quad R_0 = \Sigma\, l_x\, m_x$$

$$(5) \quad r \simeq \frac{\ln (\Sigma\, l_x\, m_x)}{T}.$$

The finite rate of growth (λ) is computed from the intrinsic rate of increase using $\lambda = e^{r\Delta t}$, where Δt is the time interval over which population change is measured. Therefore, the relative rate of population increase (or relative reproductive success among genotypes within a population) is directly dependent on fecundity, timing of reproduction, and survivorship during both the immature and adult stages (Lewontin 1965; Southwood et al. 1974; Southwood 1988; Itô 1978; Kawasaki 1980; Roff 1984; Taylor and Williams 1984; Sutherland et al. 1986; Winemiller 1992). Over long time periods and on average, the three parameters (l_x, m_x, T) must balance or the population declines to extinction or grows to precariously high densities and crashes.

Three primary life-history strategies result from trade-offs among age at maturation (α positively correlated with T), fecundity, and survivorship and are illustrated as the endpoints of a trilateral surface in Fig. 6. Here, we choose to focus attention on juvenile survivorship, the fraction of individuals surviving from the zygote stage until first reproduction. Plotting demographic trade-offs in relation to juvenile survivorship (l_α) results in separation of the equilibrium strategy of higher juvenile survivorship from the opportunistic and periodic strategies, whereas an axis of adult survivorship (the mean expectation of future life, $\bar{E}_x$, for all adult age classes, $x = a$ to ω, where $E_x = [\Sigma l_y]/l_x$ for $y = x$ to ω) would separate the opportunistic strategy

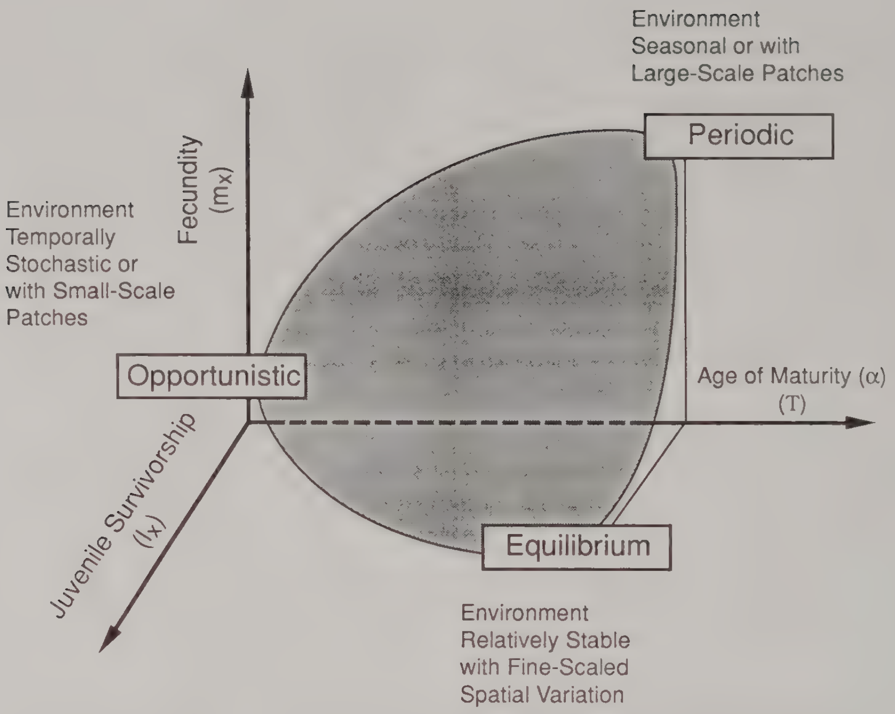

FIG. 6. Model for an adaptive surface of fish life-history strategies based on fundamental demographic trade-offs and selection in response to different kinds of environmental variation. The opportunistic strategy (small T, small m_x, small l_x) maximizes colonizing capability in environments that change frequently or stochastically on relatively small temporal and spatial scales. The periodic strategy (large m_x, large T, small l_x) is favored in environments having large-scale cyclic or spatial variation. The equilibrium strategy (large l_x, large T, small m_x) is favored in environments with low variation in habitat quality and strong direct and indirect biotic interactions. Curvilinear edges of the surface portray diminishing returns in the theoretical upper limits of bivariate relationships between adult body size and clutch size, adult body size and parental investment/offspring (a correlate of juvenile l_x), and clutch size and juvenile survivorship.

of low adult survivorship from the other two strategies. The suites of traits predicted by this adaptive surface appear similar to those described in the trichotomous comparative frameworks proposed for plants (Grime 1977, 1979) and other animal groups (Walters 1975; Allan 1976; Greenslade 1983). Our periodic strategy corresponds to high values on both the fecundity and age at maturity axes (the latter a correlate of population turnover rate) and a low value on the juvenile survivorship axis. Our opportunistic strategy (optimization of population turnover rate via a reduction in developmental time) corresponds to low values on all three axes. The equilibrium strategy is defined by low values on the fecundity axis and high values on the age at maturity and juvenile survivorship axes.

Figures 7 (freshwater) and 8 (marine) plot the positions of North American fishes in relation to three life-history variables used as surrogates (strong correlates) for the demographic axes in the trilateral gradient life-history model. Because data on size at maturation were available for more species, and size and age at maturation are highly correlated ($r = 0.77$), we used ln maturation size as a surrogate for age at maturation (x-axis). We used ln mean clutch size for fecundity (y-axis) and investment per progeny (calculated as the sum of ln parental care value and ln egg diameter) to reflect differences in the probability of juvenile survivorship (z-axis). The basic form of each empirical plot conforms well with the triangular surface predicted by the demographic model of primary life-history strategies (Fig. 6). Figures 7 and 8 strongly imply that natural selection eliminates certain combinations of life-history traits, such as late maturation/small clutches/small investment per offspring. Other combinations of life history traits, such as the ''Darwinian superorganism'' (early maturation/large clutches/large investment per offspring/long life span), are prohibited by direct physical and physiological constraints.

Response of the periodic strategy

The periodic strategy maximizes age-specific fecundity (clutch size) at the expense of optimizing turnover time (turnover times are lengthened by delayed maturation) and juvenile survivorship (maximum fecundities are attained by producing smaller eggs and larvae). Several theoretical models predict maximization of fecundity in response to predictable (= seasonal) environmental variation (Cohen 1967; Boyce 1979). If conditions favorable for growth and survival of immatures are periodic and occur at frequencies smaller than the normal life span (Southwood 1977), selection will favor the strategy of synchronous reproduction in phase with the periodicity of optimal conditions and production of large numbers of small offspring that require little or no parental care. In effect, the periodic strategy represents an iteroparous ''bet-hedging tactic'' on a scale of interannual variation.

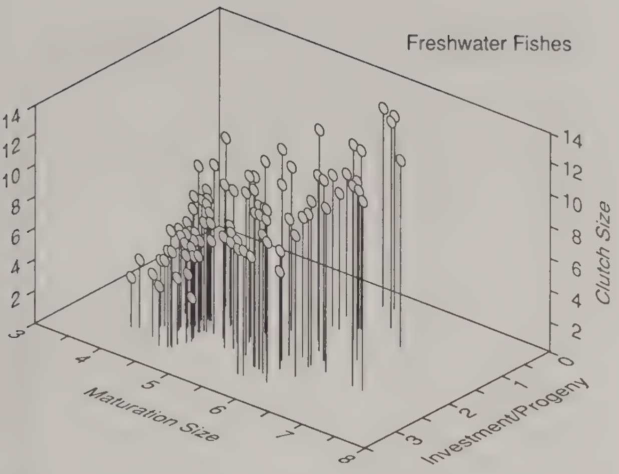

FIG. 7. Three-dimensional plot of ln maturation length (correlate of age at maturity), ln mean clutch size (fecundity), and relative investment per progeny (a surrogate for juvenile survivorship that was equal to ln ((egg diameter + 1) (parental care + 1))) for 88 freshwater fishes. The three axes permit visualization of the basic pattern of life-history variation in relation to demographic trade-offs and strategies (Fig. 6).

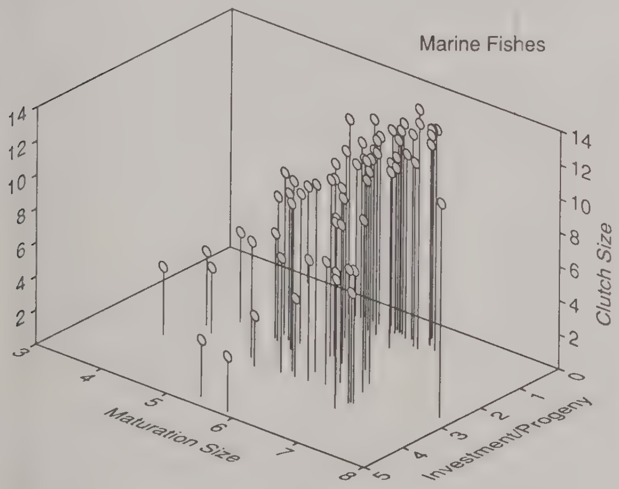

FIG. 8. Three-dimensional plot of ln maturation length, ln mean clutch, and investment per progeny for 68 marine fishes. The life-history pattern generated by marine fishes is similar to that shown by freshwater fishes (Fig. 7) and reflects essential demographic trade-offs and strategies illustrated in Figure 6.

According to this model, large body size enhances adult survivorship during suboptimal conditions and permits storage of energy and nutrients for future bouts of reproduction. The periodic production of offspring allows the organism to repeatedly sample the environment (for most perennial species, this occurs only on an annual basis) until, sooner or later, reproduction coincides with favorable conditions and the fitness payoff is collected (Murphy 1968; Armstrong and Shelton 1990). All environments exhibit either spatial or temporal variation that is to some degree predictable. This must be especially true in both freshwater and marine environments because the periodic strategy of large clutch sizes is predominant among bony fishes in both temperate and tropical settings. At arctic and temperate latitudes, the seasonal cycle appears to have selected for fish life-history cycles calibrated to annual periodicity. In marine pelagic environments, large-scale spatial patchiness of both larval food resources and predation mortality have been estimated by a variety of means (e.g. Sherman et al. 1984; McGurk 1986; Smith et al. 1989; Fortier and Gagné 1990; Brander and Hurley 1992). Large variation in the recruitment of annual cohorts appears to be the rule among periodic fishes in both marine and freshwater habitats, and the effects of climate on the distribution of larval food and predators have been implicated as principal determinants of both spatial and temporal variance in larval growth and survival (Sissenwine 1984; Fletcher and Deriso 1988; Shepherd and Cushing 1990). Variability in recruitment of several marine fishes was shown to be greater in populations closer to the latitudinal extremes of species' ranges (Myers 1992). Based on 21 marine fishes, Pepin and Myers (1991) found correlations between recruitment variability and both change in body length and duration of the larval stage. This finding is consistent with our view that the periodic strategy results in rapid growth and enhanced survival in a small fraction of initial larvae that somehow encounter zones or time periods in which food resources are abundant.

Response of the opportunistic strategy

As stated earlier, the opportunistic life-history configuration maximizes the intrinsic rate of population growth (r) through a reduction in the mean generation time (T). This reduction in T is achieved via early maturation, which in turn diminishes the capability to produce large clutches and large eggs. Owing to their small size, the relative reproductive effort of opportunistic strategists is continuously high, despite the fact that absolute clutch size and egg size are small. The production of multiple batches sometimes results in annual fecundities (mass) that greatly exceed female body mass in these small species (Wootton 1973; Hubbs 1976; Burt et al. 1988). We noted a tendency toward larger eggs and parental care in some small benthic fishes, within both freshwater and marine environments. As Mahon (1984) suggested, increasing juvenile survivorship by means of parental care may be a more viable tactic than increasing fecundity or egg size, given the material constraints imposed by small body size in these fishes. Of course, this view implies that other ecological factors (e.g. adult feeding ecology or microhabitat requirements) constrain the evolution of larger body size.

Birch (1948) was among the first to stress the strong negative correlation between population turnover time (strongly correlated with α and T) and the potential for rapid population growth in density-independent settings (high r). The advantages of early maturation for the achievement of a rapid population growth rate, and hence colonizing ability, were clearly demonstrated by Lewontin (1965), Taylor and Williams (1983), and Sibly and Calow (1986) among others. In effect, the opportunistic life history can be viewed as a sort of null life-history strategy that is favored in density-independent settings or environments that vary unpredictably on small scales of space and time. Fishes exhibiting the opportunistic strategy seem to be associated with very shallow marginal habitats: killifishes on the fringes of salt marshes and mosquitofishes in small headwater tributaries, pool edges, or swamp fringes. These shallow edge habitats (terrestrial/aquatic ecotones) are the kinds of environments that experience the largest and most unpredictable spatial and temporal changes on scales measured in days or hours. Changes in precipitation and temperature induce major alterations in water depth, substrate characteristics, and productivity in shallow aquatic habitats. The opportunistic suite of life-history charcteristics allows fishes to rebound from local disturbances in the absence of intense predation and resource limitation.

The opportunistic strategy of repeated local recolonizations through continual and rapid population turnover is well exemplified in the bay anchovy and marsh-dwelling killifishes like the mummichog. Over much of its range, the bay anchovy ranks among the most numerically dominant fishes (Morton 1989). Bay anchovies are also one of the principal food resources for a variety of fishes, birds, and invertebrates. We postulate that early maturation and frequent spawning permit the bay anchovy to sustain large numbers in regions where local subpopulations are continually cropped by predators. For bay anchovy, silversides, and other small pelagic fishes, predation pressure may partially override the signal from environmental seasonality. The opportunistic strategy appears to be more common in tropical freshwaters than in the temperate zone (Burt et al. 1988; Winemiller 1989).

Response of the equilibrium strategy

Following the basic premise of the *K*-selection theory of life histories (Pianka 1970), we postulated that the equilibrium strategy in fishes optimizes juvenile survivorship by apportioning a greater amount of material into each individual egg and/or the provision of parental care. Trade-offs between body size, egg size,and clutch size in fishes are probably inherent in the requirement for an adult body size sufficient to permit successful implementation of parental care behavior (e.g. nest defense, brooding, and gestation until larvae or embryos have attained sufficient size to escape predation or to forage efficiently). The tactic of providing parental care for a small number of offspring is of no advantage in highly seasonal habitats or environments dominated by strong density-independent selection. We believe that the equilibrium configuration of life-history traits is best understood in relation to the traditional model of density dependence and resource limitation (e.g. Pianka 1970; Roughgarden 1971; Goodman 1974). For example, some stream-dwelling darters and madtoms may experience resource limitation within shallow riffle microhabitats during periods of reduced stream flow. Microhabitats that provide refuge from predators could also be considered a resource that is either limiting or causes fishes to compete for depleted food supplies on the margins of the refuge (Fraser and Cerri 1982). In the marine environment, parental care appears to be most frequently associated with small benthic fishes (e.g. pipefishes, seahorses, some gobies, eelpouts). Among North American fishes, parental care was positively correlated with median latitude, but this trend was due to a major influence of high-fecundity marine fishes with pelagic larvae from low latitudes. Small benthic marine fishes were not well represented in the data set, and the relationship between parental care and latitude is inverse among freshwater fishes ($r = -0.36, P < 0.0001$). On a global basis, parental care appears to be most advanced and common within tropical ichthyofaunas in both freshwater (Winemiller 1989) and shallow, marine benthic environments (e.g. coral reefs; Miller 1979).

Salmon and trout life histories seem to represent variations of the equilibrium strategy that involve anadromous spawning migrations, egg hiding, and slow larval development rates rather than parental care in the traditional sense of nest guarding or brooding. The growing season at northern latitudes may be so short that large fishes are prohibited from adopting a brood guarding tactic in oligotrophic systems. Data on Arctic char (*Salvelinus alpinus*) indicated that the growing season at high latitudes probably constrains age at maturity and the frequency of spawning (Dutil 1986). Senescence associated with semelparity in Pacific salmon might have evolved as a consequence of the survival cost of returning to the sea after energetically costly upstream runs to fluvial habitats that enhance larval survivorship. By comparison, freshwater whitefishes (*Coregonus, Prosopium*) exhibit a perennial periodic strategy that involves large clutches, small eggs, and annual spawning bouts (Hutchings and Morris 1985).

Phylogenetic Trends

All life-history variables used in this study showed highly significant effects of phylogeny (Table 6). Yet, overall, the pattern of basic life-history strategies was highly repeatable within data sets containing different life-history traits and species. The high concordance between patterns revealed within this comparative study and others offers evidence that essential trade-offs produce numerous convergences in life-history strategies. For example, mouth brooding has evolved in numerous widely divergent equilibrium-type fishes worldwide (e.g. Osteoglossidae, Ariidae, Cichlidae), and miniature, multiple-clutching opportunistic-type fishes are found within many large families, especially in shallow environments in the tropics (e.g. Characidae, Cyprinidae, Cyprinodontidae, Gobiidae). Formal phylogentic studies of life-history evolution would contribute immensely to our understanding of the scenarios favoring the evolution of specific life-history strategies (Gotelli and Pyron 1991).

The restriction of some phylogenetic clades to subregions of life-history space results from historical events shaping evolution, morphological and physiological design constraints, and the interaction of these with contemporary ecology. Despite the reality of phylogentic constraints, wide divergence within several higher taxa is apparent in plots of species scores in relation to the life-history continua that were reflected in the principal axes from PCA (Fig. 3, 4). Perciforms are a widely divergent group, particularly within the freshwater data set. Cypriniforms exhibit a wide range of strategies primarily along an axis linking the periodic and opportunistic endpoints. Salmoniforms show a range of strategies along an axis between a periodic strategy and an intermediate strategy located midway between the equilibrium and periodic extremes. In the marine group, clupeiforms span an axis between opportunistic and periodic strategies, and gadiforms span an axis between the periodic and equilibrium strategy endpoints. Several other orders show much greater restrictions in their ranges of life-history strategies (e.g. percopsiforms tended to be equilibrium strategists, acipenseriforms and pleuronectiforms were relative periodic strategists).

Life-History Strategies and Fisheries Management

Life-history theory can provide some general insights into where attention might be most profitably focused in monitoring and research (Adams 1980; Garrod and Horwood 1984; Ware 1984; Schaaf et al. 1987; Barnthouse et al. 1990; Leaman 1991). For example, the periodic strategy is designed to exploit differences in environmental quality on temporal and spatial scales that are relatively large and to some degree regular or predictable. We have noted that the periodic strategy is predominant among commercial fish stocks worldwide. At arctic and temperate latitudes where spawning is largely annual and synchronous, generations are often recognizable as fairly discrete age cohorts. Correlations between parental stock densities and densities of YOY recruits are frequently weak or negligible in periodic strategists (Garrod 1983; Fletcher and Deriso 1988; Shepherd and Cushing 1990). Consequently, fisheries projections rely on juvenile cohort estimates as short-term forecasters of catchable stocks.

We view the periodic strategy as the perennial tactic of spreading reproductive effort over many years (or over a large area), so that high larval/juvenile survivorship during one year (or in one spatial zone) compensates for the many bad years (or zones). For example, anadromous female striped bass live up to 17 yr on average and produce an average clutch of 4×10^6 eggs every year or two, which translates to an egg to maturation survivorship of roughly 3×10^{-8} to maintain an equilibrium population. We speculate that most years probably result in a larval survivorship approaching zero for most females. From the standpoint of an individual female, it is likely that the fitness payoff only comes during one or two spawning acts over the course of a normal life span. These extremely low expectations for larval survivorship are far smaller than measurement errors involved with field estimates of mortality. In species like striped bass, the variance in larval survivorship that serves as input for population projections lies well beyond our ability to measure differences in the field (Koslow 1992). The maintenance of some critical density of adult stocks and the protection of spawners and spawning habitats during the short reproductive period should be crucial in the management of long-lived periodic fishes. If most larvae never recruit into the adult population even under pristine conditions, it follows that spawning must proceed unimpeded each year in fairly undegraded habitats if a fitness payoff is to be collected during the exceptional year.

Because they tend to be small and occur in shallow shoreline habitats, opportunistic strategists are not usually exploited commercially. Some species intermediate between opportunistic and periodic are very important commercial stocks (e.g. gulf menhaden (*Brevoortia patronus*)). Yet, opportunistic species are often the most important food resources for larger piscivorous species. By virtue of their small size and rapid turnover rates, these species should be efficient colonizers of frequently disturbed habitats like intermittent streams and salt marshes. Some opportunistic strategists, like the bay anchovy and silversides, inhabit more stable habitats and sustain dense populations in the face of intense predation. Given the innate ability of opportunistic strategists to sustain losses during all stages of life spans that are typically rather short, one of the keys to their management might be protection from large-scale or chronic perturbations that eliminate key refugia in space or time. Obviously, what may be perceived by humans to be a minor disturbance (e.g. a few degrees centigrade, or a few parts per thousand salinity) might pose a major impact from the perspective of a small fish that must maintain high reproductive output over a short life span.

Because equilibrium strategists produce small numbers of offspring, larval and juvenile survivorship must be comparatively high if these populations are to maintain themselves around some average density. Parental care is often well developed in equilibrium strategists, so that survivorship of eggs and larvae is dependent on the condition of adults and the integrity of the adult habitat (e.g. threatened cavefishes and some species of darters and madtoms). These fishes ought to conform to stock–recruit fishery models to a greater extent than periodic and opportunistic strategists (and see Koslow (1992) for a discussion of the effect of fecundity on the stock–recruit relationship). Yet, relatively few equilibrium strategists are commercially exploited in North American marine and freshwaters. Several species exploited by sport fisheries exhibit brood guarding and appear to be intermediate between equilibrium and periodic strategies, including lingcod (*Ophiodon elongatus*) and the black basses (*Micropterus* spp.). In general terms, management of these larger equilibrium-type species should be aimed at maintenance of a productive environment that promotes surplus yields (which can be harvested and replaced via compensation) and the maintenance of healthy adult stocks. We suggested that anadromous salmonids could represent a variation on the equilibrium strategy, in which parental investment in the form of costly migrations to oligotrophic habitats take the place of guarding, brooding, or bearing. Following this view, degradation of spawning habitats or impedement of access to spawning sites would have the same net impact as removing nest-guarding or brooding adults during the spawning season.

Finally, we point out that a variety of fishes with divergent life-history strategies frequently coexist in the same habitats. The feeding niche probably determines a large proportion of the total environmental variance experienced by an organism. Inherited design constraints, including the morphological features required for trophic function in particular microhabitats, place restrictions on the evolution of life-history features. A diversity of life-history strategies are consequently observed among species that perceive the same environment very differently from another. As a consequence, management efforts designed to abate a problem for a given species may sometimes have unanticipated effects on sympatric species that exhibit alternative strategies.

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Appendix: List of Fishes Used in Statistical Analyses

Freshwater

Lake sturgeon, *Acipenser fulvescens*; paddlefish, *Polyodon spathula*; longnose gar, *Lepisosteus osseus*; bowfin, *Amia calva*; goldeye, *Hiodon alosoides*; gizzard shad, *Dorosoma cepedianum*; threadfin shad, *Dorosoma petenense*; cisco/lake herring, *Coregonus artedi*; lake whitefish, *Coregonus clupeaformis*; bloater, *Coregonus hoyi*; sockeye salmon, *Oncorhynchus nerka kennerlyi*; round whitefish, *Prosopium cylindraceum*; mountain whitefish, *Prosopium willamsoni*; brook trout,[3] *Salvelinus fontinalis*; lake trout,[3] *Salvelinus namaycush*; Arctic grayling, *Thymallus arcticus*; Alaska blackfish, *Dallia pectoralis*; central mudminnow, *Umbra limi*; redfin pickerel, *Esox americanus americanus*; northern pike, *Esox lucius*; muskellunge, *Esox masquinongy*; chain pickerel, *Esox niger*; central stoneroller, *Campostoma anomalum*; redside dace, *Clinostomus elongatus; spotfin shiner, Cyprinella spiloptera*; Utah chub, *Gila atraria*; Mississippi silvery minnow, *Hybognathus nuchalis*; hornyhead chub, *Nocomis biguttataus*; golden shiner, *Notemigonus crysoleucas*; emerald shiner, *Notropis atherinoides*; spottail shiner, *Notropis hudsonius*; rosyface shiner, *Notropis rubellus*; sand shiner, *Notropis stramineus*; redfin shiner, *Lythrurus umbratilis*; bluntnose minnow, *Pimephales notatus*; fathead minnow, *Pimephales promelas*; northern squawfish, *Ptychocheilus oregonensis*; blacknose dace, *Rhinichthys atratulus*; longnose dace, *Rhinichthys cataractae*; redside shiner, *Richardsonius balteatus*; creek chub, *Semotilus atromaculatus*; river carpsucker, *Carpoides carpio*; longnose sucker, *Catotstomus catostomus*; white sucker, *Catostomus commersoni*; mountain sucker, *Catostomus platyrhynchus*; lake chubsucker, *Erimyzon sucetta*; smallmouth buffalo, *Ictiobus bubalus*; bigmouth buffalo, *Ictiobus cyprinellus*; silver redhorse, *Moxostoma anisurum*; black redhorse, *Moxostoma duquesnei*; golden redhorse, *Moxostoma erythrurum*; shorthead redhorse, *Moxostoma macrolepidotum*; black bullhead, *Ameiurus melas*; yellow bullhead, *Ameiurus natalis*; brown bullhead, *Ameiurus nebulosus*; channel catfish, *Ictalurus punctatus*; Ozark madtom, *Noturus albater*; stonecat, *Noturus flavus*; tadpole madtom, *Noturus gyrinus*; brindled madtom, *Noturus miurus*; freckled madtom, *Noturus nocturnus*; flathead catfish, *Pylodictis olivaris*; Ozark cavefish, *Amblyopsis rosae*; northern cavefish, *Amblyopsis spelaea*; spring cavefish, *Chologaster agassizi*;

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[3] The authors prefer the term "char."

swampfish, *Chologaster cornuta*; southern cavefish, *Typhlichthys subterraneus*; pirate perch, *Aphredoderus sayanus*; trout-perch, *Percopsis omiscomaycus*; burbot, *Lota lota*; banded killifish, *Fundulus diaphanus*; plains killifish, *Fundulus zebrinus*; western mosquitofish, *Gambusia affinis*; freshwater drum, *Aplodinotus grunniens*; white bass, *Morone chrysops*; rock bass, *Ambloplites rupestris*; flier, *Centrarchus macropterus*; banded pygmy sunfish, *Elassoma zonatum*; redbreast sunfish, *Lepomis auritus*; green sunfish, *Lepomis cyanellus*; pumpkinseed, *Lepomis gibbosus*; warmouth, *Lepomis gulosus*; orangespotted sunfish, *Lepomis humilis*; bluegill, *Lepomis macrochirus*; longear sunfish, *Lepomis megalotis*; redear sunfish, *Lepomis microlophus*; smallmouth bass, *Micropterus dolomieu*; spotted bass, *Micropterus punctulatus*; largemouth bass, *Micropterus salmoides*; white crappie, *Pomoxis annularis*; black crappie, *Pomoxis nigromaculatus*; naked sand darter, *Ammocrypta beani*; greenside darter, *Etheostoma blennioides*; rainbow darter, *Etheostoma caeruleum*; Iowa darter, *Etheostoma exile*; fantail darter, *Etheostoma flabellare*; yoke darter, *Etheostoma juliae*; greenthroat darter, *Etheostoma lepidum*; johnny darter, *Etheostoma nigrum*; tessellated darter, *Etheostoma olmstedi*; orangethroat darter, *Etheostoma spectabile*; variegate darter, *Etheostoma variatum*; banded darter, *Etheostoma zonale*; yellowperch, *Perca flavescens*; logperch, *Percina caprodes*; blackside darter, *Percina maculata*; slenderhead darter, *Percina phoxocephala*; dusky darter, *Percina sciera*; sauger, *Stizostedion canadense*; walleye, *Stizostedion vitreum*; slimy sculpin, *Cottus cognatus*.

Marine

Shortnose sturgeon, *Acipenser brevirostrum*; Atlantic sturgeon, *Acipenser oxyrhynchus*; ladyfish, *Elops saurus*; tarpon, *Megalops atlanticus*; American eel, *Anguilla rostrata*; blueback herring, *Alosa aestivalis*; alewife, *Alosa pseudoharengus*; American shad, *Alosa sapidissima*; gulf menhaden, *Brevoortia patronus*; Atlantic menhaden, *Brevoortia tyrannus*; Atlantic herring, *Clupea harengus*; Pacific sardine, *Sardinops sagax*; bay anchovy, *Anchoa mitchilli*; anchoveta, *Cetengraulis mysticetus*; northern anchovy, *Engraulis mordax*; cutthroat trout, *Oncorhynchus clarki*; pink salmon, *Oncorhynchus gorbuscha*; chum salmon, *Oncorhynchus keta*; coho salmon, *Oncorhynchus kisutch*; rainbow trout/steelhead, *Oncorhynchus mykiss*; chinook salmon, *Oncorhynchus tshawytscha*; Atlantic salmon, *Salmo salar*; Arctic char, *Salvelinus alpinus*; Dolly Varden, *Salvelinus malma*; capelin, *Mallotus villosus*; rainbow smelt, *Osmerus mordax*; longfin smelt, *Spirinchus thaleichthys*; eulachon, *Thaleichthys pacificus*; hardhead catfish, *Arius felis*; gafftopsail catfish, *Bagre marinus*; plainfin midshipman, *Porichthys notatus*; oyster toadfish, *Opsanus tau*; Pacific cod, *Gadus macrocephalus*; Atlantic cod, *Gadus morhua*; Pacific hake, *Merluccius productus*; Atlantic tomcod, *Microgadus tomcod*; red brotula, *Brosmophycis marginata*; blackbelly eelpout, *Lycodopsis pacifica*; California grunion, *Leuresthes tenuis*; inland silverside, *Menidia beryllina*; Atlantic silverside, *Menidia menidia*; mummichog, *Fundulus heteroclitus*; tubesnout, *Aulorhynchus flavidus*; threespine stickleback, *Gasterosteus aculeatus*; ninespine stickleback, *Pungitius pungitius*; gulf pipefish, *Syngnathus scovelli*; skipjack tuna, *Katsuwonus pelamis*; chub mackerel, *Scomber japonicus*; Atlantic mackerel, *Scomber scombrus*; Atlantic threadfin, *Polydactylus octonemus*; Pacific barracuda, *Sphyraena argentea*; cobia, *Rachycentron canadum*; American sand lance, *Ammodytes americanus*; northern sand lance, *Ammodytes dubius*; jack mackerel, *Trachurus symmetricus*; bluefish, *Pomatomus saltatrix*; tomtate, *Haemulon aurolineatum*; white grunt, *Haemulon plumieri*; pigfish, *Orthopristis chrysoptera*; spotted seatrout, *Cynoscion nebulosus*; weakfish, *Cynoscion regalis*; spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogonias undulatus*; red drum, *Sciaenops ocellatus*; pinfish, *Lagodon rhomboides*; scup, *Stenotomus chrysops*; black grouper, *Mycteroperca bonaci*; red grouper, *Epinephelus morio*; Nassau grouper, *Epinephelus striatus*; black sea bass, *Centropristis striata*; red snapper, *Lutjanus campechanus*; tautog, *Tautoga onitis*; common snook, *Centropomus undecimalis*; white perch, *Morone americana*; striped bass, *Morone saxatilis*; shiner perch, *Cymatogaster aggregata*; striped seaperch, *Embiotoca lateralis*; walleye surfperch, *Hyperprosopon argenteum*; rubberlip seaperch, *Rhacochilus toxotes*; pile perch, *Rhacochilus vacca*; high cockscomb, *Anoplarchus purpurescens*; arrow goby, *Clevelandia ios*; clown goby, *Microgobius gulosus*; coastrange sculpin, *Cottus aleuticus*; showy snailfish, *Liparis pulchellus*; Pacific ocean perch, *Sebastes alutus*; brown rockfish, *Sebastes auriculatus*; copper rockfish, *Sebastes caurinus*; splitnose rockfish, *Sebastes diploproa*; yellowtail rockfish, *Sebastes flavidus*; chilipepper, *Sebastes goodei*; shortbelly rockfish, *Sebastes jordani*; black rockfish, *Sebastes melanops*; bocaccio, *Sebastes paucispinis*; canary rockfish, *Sebastes pinniger*; stripetail rockfish, *Sebastes saxicola*; shortspine thornyhead, *Sebastolobus alascanus*; lingcod, *Ophiodon elongatus*; gulf flounder, *Paralichthys albigutta*; California halibut, *Paralichthys californicus*; summer flounder, *Paralichthys dentatus*; southern flounder, *Paralichthys lethostigma*; flathead sole, *Hippoglossoides elassodon*; Pacific halibut, *Hippoglossus stenolepis*; rock sole, *Pleuronectes bilineatus*; Dover sole, *Microstomus pacificus*; English sole, *Pleuronectes* starry flounder, *Platichthys stellatus*; winter flounder, *Pleuronectes americanus*; ocean sunfish, *Mola mola*.

ANNOUNCEMENTS/AVIS

American Society of Limnology and Oceanography (ASLO) and the Society of Wetland Scientists (SWS)

University of Alberta, Edmonton, Alberta, Canada
May 30 to June 3, 1993

Announcement of Annual Meeting and Conference

The first joint meeting of ASLO and SWS is scheduled for May 30 to June 3, 1993, at the University of Alberta, Edmonton, Alberta, Canada. The major theme of the conference is "Freshwater, marine, and wetland interfaces: dynamics and management." There are several proposed topics and papers will be considered on all topics related to the conference. Some of the proposed topics include

- Large floodplain rivers — dynamics and human impacts
- Effect of climate change on marine and freshwater systems
- Physical/biological coupling in marine and freshwater systems
- Restoration ecology of estuaries, lakes, rivers, and wetlands
- Ecology and management of wetlands on permafrost
- Land/ocean interactions
- Impact of pulp mill operations on marine and freshwater ecosystems
- Ecology and management of contaminated ecosystems
- Sediment/water geochemistry of aquatic and peatland systems
- Paleoecology

and many, many more. Authors are encouraged to submit papers on these and other topics, as well as posters.

Call for papers will be sent to members in late September 1992. The deadline for abstracts is **December 31, 1992**.

There are four tours proposed leading up to or following the conference:

- Rocky Mountains: Banff – Lake Louise – Jasper corridor
- Boreal peatlands and lakes
- Saline lakes and irrigation
- Royal Tyrrell Museum of Paleontology

Prior to the ASLO/SWS Conference, NABS will be meeting in Calgary May 23–27, 1993. For more information, contact Dr. Fred Wrona at (306) 975-6099. Following the ASLO/SWS Conference is GAP VI in Saskatoon, June 7–15, 1993. Buses are available. For more information, contact Dr. Richard Robarts at (306) 975-6047.

Conference cosponsors include the Freshwater Institute, the Society of Canadian Limnologists, the NHRI/Rawson Academy of Aquatic Science, and Alberta Environment.

For further details, and to put your name on the mailing list, write to ASLO/SWS 1993 Conference, Environmental Research & Studies Centre, University of Alberta, CW-401L BioSciences Building, Edmonton, Alta. T6G 2E9, Canada. FAX: (403) 492-8160.

Réunion annuelle et conférence de l'American Society of Limnology and Oceanography (ASLO) et de la Society of Wetland Scientists (SWS)

Université de l'Alberta, Edmonton (Alberta), Canada
du 30 mai au 3 juin 1993

Annonce de la réunion annuelle et de la conférence

La première réunion conjointe de l'ASLO et de la SWS sera tenue du 30 mai au 3 juin 1993 à l'Université de l'Alberta, Edmonton (Alberta), Canada. La conférence aura pour thème principal «Interfaces eaux douces, mer et terres humides: dynamique et gestion». Plusieurs sujets sont proposés et des communications traitant de tous les sujets peuvent être présentées. Les sujets proposés comprennent notamment :

- Fleuves des plaines inondables — Dynamique et incidences humaines
- Effet du changement climatique sur les systèmes marins et d'eau douce
- Association physique et biologique des systèmes marins et d'eau douce
- Restauration de l'écologie des estuaires, des lacs, des cours d'eau et des terres humides
- Écologie et gestion des terres humides sur pergélisol
- Interactions terre–mer
- Incidences des usines de pâte sur les écosystèmes marins et dulcicoles
- Écologie et gestion des écosystèmes contaminés
- Géochimie des sédiments et de l'eau des systèmes aquatiques et des tourbières
- Paléo-écologie

etc. Les auteurs sont invités à présenter des communications, et des affiches, sur ces sujets ou d'autres sujets connexes.

Les demandes de communications seront transmises aux membres à la fin de septembre. Les résumés doivent être expédiés au plus tard **le 31 décembre 1992**.

Quatre sorties organisées sont prévues avant ou après la Conférence. Ce sont :

- Les Rocheuses: corridor Banff – lac Louise – Jasper
- Tourbières et lac boréaux
- Lacs salins et irrigation
- Royal Tyrrell Museum of Paleontology

La NABS tiendra une réunion à Calgary du 23 au 27 mai 1993, soit avant la conférence conjointe ASLO et SWS. Pour plus de précisions à ce sujet, veuillez entrer en relation avec le Dr. Fred Wrona, au (306) 975-6099. La conférence ASLO-SWS sera suivie du GAP VI, qui se tiendra à Saskatoon, du 7 au 15 juin 1993. Le transport sera assuré par autobus. Des renseignements supplémentaires peuvent être obtenus du Dr. Richard Robarts, au (306) 975-6047.

La conférence est parrainée par l'Institut des eaux douces, la Société canadienne de limnologie, l'Académie NHRI/Rawson des sciences de l'eau et Alberta Environment.

Pour obtenir des renseignements supplémentaires ou faire

Implementing Integrated Environmental Management

March 9 to 11, 1993
Donaldson Brown Center for Continuing Education,
Virginia Polytechnic Institute and State University,
Blacksburg, Virginia, USA

Co-conveners

John Cairns, Jr. (Virginia Polytechnic Institute and State University), Todd V. Crawford (Westinghouse, Savannah River Laboratory), and Hal Salwasser (United States Department of Agriculture).

This two and a half day workshop will consist of approximately 20 speakers who will present aspects of decisions on complex environmental management issues requiring integration of a variety of interests.

In much of the legal, regulatory, and academic arenas, environmental considerations are usually media specific (air, surface water, groundwater, wetlands, endangered species, etc.) and yet, environmental management decisions that are multimedia must be made. Concepts of and solutions to case studies were previously explored by the co-convenors in a conference entitled ''Integrated Environmental Management'' held in September 1989 in Aiken, South Carolina, that resulted in the publication of the book *Integrated Environmental Management* by Lewis Publishers. The present workshop is aimed at an audience, such as environmental policymakers, planners, managers, scientists, educators, and lobbyists, who can influence implementation of these concepts and solutions. Case studies of successes and failures of integrated environmental management will be presented, followed by panel discussions. These actual examples of integrated environmental management document practical applications and present lessons for environmental science, education, laws and regulations, planning, and management. This use of real examples will provide an effective communication vehicle. Lewis Publishers will be publishing the book that results from this workshop.

The registration fee is $150.00 per person. This fee includes two banquet meals, refreshment breaks, and a copy of the book that results from the workshop. Advanced registration and payment are required no later than **February 15, 1993**. Registrations after this date must be confirmed with the Conference Registrar at (703) 231-5182 to verify space availability.

For more information about the workshop, contact John Cairns, Jr. (703) 231-5538. For more information on registration or lodging, contact Roy Jones (703) 231-5242.

ajouter votre nom à liste d'expédition, veuillez écrire à : Conférence ASLO-SWS de 1993, Environmental Research and Studies Centre, University of Alberta, CW-401L, BioSciences Building, Edmonton (Alberta) T6G 2E9, Canada. Télécopieur : (403) 492-8160.

Mise en oeuvre d'une gestion intégrée de l'environnement

du 9 au 11 mars 1993
Donaldson Brown Center for Continuing Education,
Virginia Polytechnic Institute and State University,
Blacksburg (Virginie) (États-Unis)

Co-responsables

John Cairns (Virginia Polytechnic Institute and State University), Todd V. Crawford (Westinghouse, Savannah River Laboratory) et Hal Salwasser (Department of Agriculture des États-Unis).

Cet atelier d'une durée de deux jours et demi fera intervenir environ vingt orateurs qui présenteront des aspects des décisions prises en ce qui concerne des questions complexes pour la gestion de l'environnement et qui exigent l'intégration de différents intérêts.

Dans la plupart des domaines juridiques, réglementaires et universitaires, les considérations en matière d'environnement sont d'ordinaire propres à un médium précis (air, eaux de surface, eaux souterraines, terres humides, espèces menacées, etc.) et, malgré tout, des décisions en matière de gestion de l'environnement qui intéressent plusieurs médiums doivent être prises. Les notions et les solutions propres à des études de cas ont antérieurement été étudiées par les co-responsables d'une conférence intitulée « Integrated Environmental Management » qui a eu lieu en septembre 1989 à Aiken (Caroline du Sud) et qui a donné lieu à la publication d'un livre intitulé *Integrated Environmental Management*, par la firme Lewis Publishers. Le présent atelier est destiné à une audience comme des décideurs sur le plan de l'environnement, des planificateurs, des gestionnaires, des scientifiques, des éducateurs et des lobbyistes, qui peuvent influer sur la mise en oeuvre de ces notions et solutions. Des études de cas d'entreprises fructueuses et infructueuses en matière de gestion intégrée de l'environnement seront présentées, et suivies de discussions en comité. Ces exemples réels de gestion intégrée de l'environnement permettent de documenter des applications pratiques et des leçons actuelles pour la science de l'environnement, l'éducation, les lois et les règlements, la planification et la gestion. Le recours à des exemples réels permettra d'établir un mécanisme de communication efficace. La firme Lewis Publishers publiera le livre qui résultera de cet atelier.

Les frais d'inscription sont de 150 $ par personne. Ces frais comprennent deux repas, les boissons aux pauses, et un exemplaire du livre qui sera publié d'après les résultats de l'atelier. L'inscription et le paiement anticipés sont requis pour **le 15 février 1993**, au plus tard. Les inscriptions après cette date doivent être confirmées auprès du secrétaire de la Conférence au numéro (703) 231-5182, pour permettre de vérifier les places disponibles.

Pour obtenir d'autres renseignements sur l'atelier, veuillez communiquer avec John Cairns, Jr. au numéro (703) 231-5538. Pour obtenir d'autres renseignements sur l'inscription ou l'hébergement, veuillez communiquer avec Roy Jones au numéro (703) 231-5242.

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 49, No. 10, October 1992 **Volume 49, n° 10, octobre 1992**

Irvine, J. R., R. C. Bocking, K. K. English, and M. Labelle. Estimating coho salmon (*Oncorhynchus kisutch*) spawning escapements by conducting visual surveys in areas selected using stratified random and stratified index sampling designs **1972–1981**

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Gordoa, A., and C. M. Duarte. Size-dependent density of the demersal fish off Namibia: patterns within and among species **1990–1993**

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